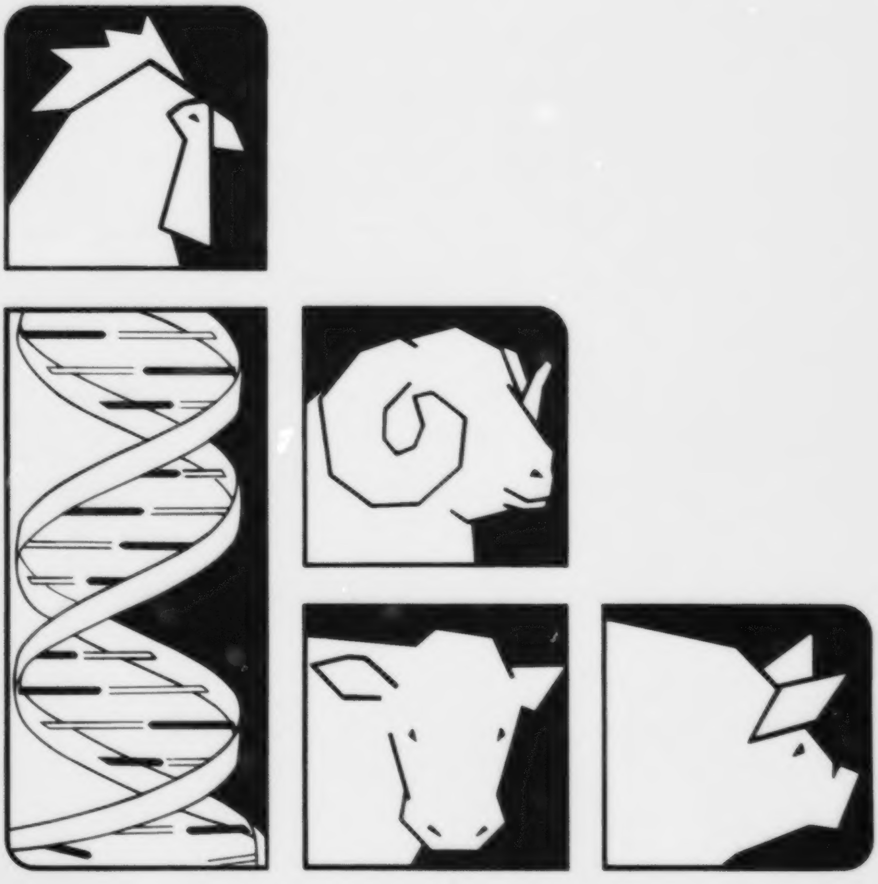
Agriculture
Canada

Animal Breeding

Recent Advances and Future Prospects



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PREFACE

The overall purpose of this review was to provide a picture of the total area of animal breeding, which, to the authors' knowledge, has not previously been available. To attempt this task by a single author appeared extremely difficult. A group of scientists has therefore collaborated in this review. The target audience was defined as the general community of geneticists, particularly those working outside animal breeding. The review may be particularly useful to those entering the field of animal improvement, as well as to research managers and to funding bodies. Finally, the authors present a large number of references, which will have value as a bibliography of animal breeding.

Presented in part at the Symposium "Genetics in Agriculture" at the 1983 Annual meetings of the Genetics Society of Canada.

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INTRODUCTION

J.S. Gavora

Animal breeding is one of the oldest human activities related to the acquisition of food and clothing. Alteration of domesticated species by selective breeding to produce breeds and types better suited for serving human needs predates the emergence of animal breeding as a scientific discipline. Most of today's animal and poultry breeds already existed at the beginning of the 20th century when scientific bases for today's animal breeding theory were being formulated. The contrasting breeds that were diversified within species of domesticated animals are exemplified today in cattle by the dairy and beef breeds and in chickens by the meat- and egg-producing types. Similar dramatic morphological and physiological differences are found among breeds of swine and sheep. The common denominator in most of the historical breeds is that their formation took a long time. Periods for their development ranged in the order of tens to hundreds of years. In many instances the exact origin of old breeds is, because of historical distance, uncertain.

Manipulation of both the reproductive process and the animal genome made possible by recent scientific developments is now demonstrating the possibilities of introducing dramatically rapid, morphological and physiological changes. For example, the increase in body size of mice that was obtained by injecting eggs with rat growth hormone genes (Palmiter et al. 1982*a*) is comparable to differences in body size between breeds of horses such as the Percheron and the Shetland pony. Yet, it was achieved virtually "overnight." Thus, genetics and animal breeding have entered a completely new era in which qualitatively different techniques to manipulate genetic material are becoming available. They can be expected eventually to allow changes that may be beyond our imagination at present. At the same time, the rapidly growing understanding of the genome and its complexity is challenging what was believed to be unique to biological systems. Genetic instructions encoded in a linear fashion within the genome represent information to which general principles and techniques of information theory can be applied.

Despite great progress achieved by genetics in the past two decades, we are only beginning to understand the functioning of genes in eukaryotes and have very little knowledge about the syntax and grammar of the genome. The state of our present understanding of the genome is reminiscent of the situation of the young Tarzan, the protagonist in a series of 23 books (1912–19) by Edgar Rice Burrows, in which the life of a human male raised from childhood by apes in a jungle is described. When, as a boy in the wilds, Tarzan first discovered his parents' books, he quickly learned to recognize individual letters and even simple, repeated words. Gradually he was able to understand the meaning of larger words, sentences, and text in its entirety. Eventually, through perseverence, he became literate and returned to civilization. Geneticists are, like the boy Tarzan, only at the beginning of their quest for understanding the genome at the molecular level. Nevertheless, the process has undoubtedly begun and continues.

The forthcoming changes, their potential effects on animal breeding, and the need to balance the use of conventional methods with the new approaches are the basic motivation for undertaking the compilation of this review. The most recent similar review in Canada was by Fredeen, published in 1977. In 1982, Skjervold, as part of a symposium devoted to future developments in the genetic improvement of animals, reviewed the results of the past 20 years of cattle, sheep, and pig breeding and suggested answers to the question "Which way now?" He concluded that the past 20 years gave good results in animal breeding, with increasing rate of genetic improvement. He predicted that new techniques such as biophysical profiling, embryo manipulation, genetic engineering, computer tomography, and multibreed mating strategies may become commonplace before the end of the century. Dickerson and Willham (1983) considered the past and future of genetic engineering for more efficient animal production. They pointed out several important findings, resulting from theoretical work, computer simulation, and animal experimentation: large numbers of genes control quantitative traits; adverse pleiotropic or epistatic effects on reproductive traits result from extreme selection for metric traits; loss of previous genetic gain occurs with relaxed selection; population size and structure, information on relatives, accurate economic weights, and genetic parameters are important considerations for successful selection.

The statement by Fredeen (1977) that the science of animal breeding has progressed far beyond its practical application, is perhaps more valid today than ever before. A careful examination of past accomplishments and future prospects should, therefore, be useful for continued improvement of domestic animals.

The general objectives of this review are to:

- evaluate critically the progress achieved in animal breeding practice and research over the past two decades for the basic species of domestic animals and poultry;
- identify the major factors that contributed to the progress;
- project the future route for genetic improvements;
- identify important areas that require particular attention and emphasis; and
- examine the role of the various scientific disciplines or areas of research related to animal improvement from the points of view of their past and future effects and interactions.

IMPORTANCE OF ANIMAL PRODUCTS

Table 1 shows the size of populations of cattle, sheep, swine, and chickens for Canada, North America (Canada, the United States, and Mexico), and the world, as well as the numbers of these animals in relation to human populations (FAO–WHO–OIE 1986). The animal species considered here are limited to these four because the remaining species, such as camels, goats, llamas, turkeys, and rabbits, are relatively insignificant, especially globally.

Omission of aquatic species could be considered unjustified, as they represent a significant and growing proportion of food from animals. Furthermore, application of animal breeding techniques to the improvement of fish and shellfish for aquaculture will likely be of great future importance in human nutrition. Evaluation of selection experiments indicates that possibilities for genetic improvement are good in fish (Gjedrem 1983). However, this review does not deal with this newly emerging area.

The large size of the world's animal populations documents their importance in providing food for humans; some areas of the world, for example parts of Asia, Australia, and Africa are used almost exclusively for animal agriculture. Only about 11.5% of the world's land can be used to produce cereal crops; twice that amount is available for pasturing animals. The rising affluence of human populations, particularly in the northern hemisphere, is increasing the proportion of food supplied by animals. For example, more than 40% of the food supply in the United States is now of animal origin.

Whereas most food of plant origin is believed to be produced from 15 to 20 plant species, most food of animal origin is produced from only four species. This narrow species base allows a focusing of

Table 1 Size of animal populations

	Total No. (millions)			Per 100 inhabitants		
Species	Canada	North and Central America	World	Canada	North and Central America	World
Cattle	11.5	171	1272	44	42	26
Sheep	0.7	21	1146	3	5	23
Swine	10.7	91	822	41	22	17
Chickens	99.3	1602	8924	382	394	181

Source: FAO–WHO–OIE 1986.

animal research and an application of new findings and improvements to large populations, limited only by environmental differences. As modern animal production becomes gradually less dependent on natural environment (e.g., poultry and swine), global application of important findings becomes increasingly feasible. Because of the large size of animal populations, and because of their cumulative nature, even small genetic improvements can result in large economic benefits.

The small number of important domestic animal species also points out the high vulnerability of global animal production. Emergence of highly virulent pathogens, for example the virus of foot-and-mouth disease, can decimate large animal populations. Another danger connected with the small number of important domestic animal species that exists is the reduction of available genetic variation that results from the extinction of breeds, strains, and lines. Narrowing the genetic base of important species of livestock may be particularly dangerous when low-producing indigenous breeds are replaced by imports of modern, highly productive stocks. Important disease resistance genes may be lost by such substitutions.

International activities aimed at the preservation of animal resources date back to 1960, when the Food and Agriculture Organization of the United Nations (FAO) originated a series of expert consultations on the subject. Subsequent activities organized by FAO and the United Nations environment program (UNEP) included another technical consultation in 1980 and launching of a newsletter *Animal Genetic Resources Information* in 1983. Current activities by FAO/UNEP include organization of data banks for animal genetic resources, gene banks to store frozen semen and embryos, surveys of lesser known breeds, training of scientists and administrators in animal resources conservation and size, and others (Hodges 1986). Efforts to conserve and manage animal gene resources lag far behind those in plants. The concerns concentrate on developing countries and do not pay much attention to the narrowing genetic base of some domestic species in developed countries. Land (1986), in fact, argued that "...the premise that population must be conserved to maintain genetic diversity and the option for future change is false. Furthermore, even if populations were conserved, it is unlikely that they could be used effectively."

The narrowing down of the genetic base has progressed perhaps furthest in turkey breeding. Only three or four breeding companies now supply turkey poults to almost all the world's turkey producers. This situation, if it persists, may be dangerous because, at least for the foreseeable future, the substitution of lost genetic material by synthetic new genes is not feasible. This shortcoming, along with pressure from circles outside animal breeding advocating preservation of germ plasm on philosophical and ethical grounds, should attract more attention to this issue especially now that modern methods of gamete and zygote cryopreservation are becoming available and practical (Crawford 1984).

ANIMAL BREEDING INDUSTRIES

Figure 1 shows schematically the relationship between the female reproductive rate of the main four domestic animal species and the number of breeders or breeding companies. In cattle, particularly dairy cattle, almost every producer is also a breeder. On the other hand, genetic improvement of commercial chickens in the world is concentrated in the hands of less than 20 large breeding companies. This vast difference in the number of breeders dictates a completely different organization of the two breeding industries.

The improvement programs for species with large numbers of breeders are usually run by national or regional organizations, most of which have a strong element of government intervention. Genetic and breeding expertise is primarily available at the headquarters of the organization. More-or-less uniform recording and selection criteria are applied throughout the subject region. In dairy cattle,

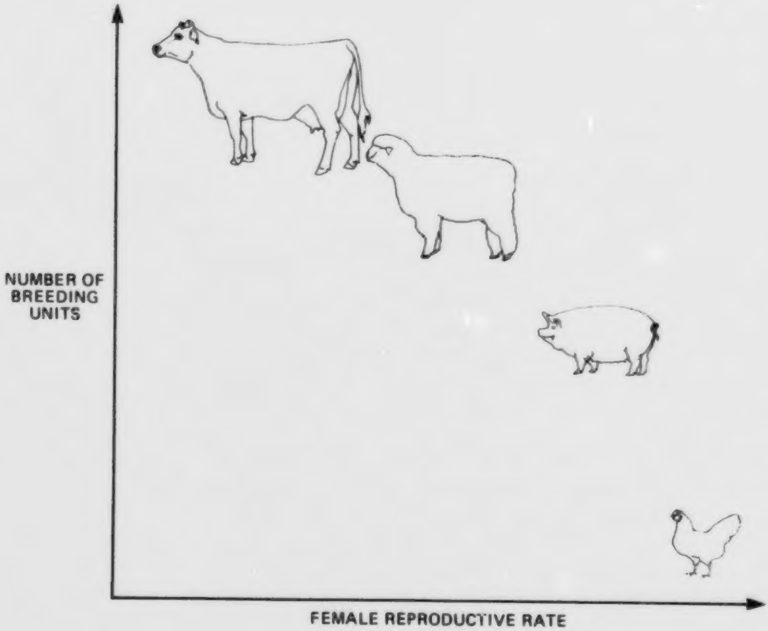

Figure 1 Relationship between female reproductive rate and number of breeding establishments for cattle, sheep, swine, and chickens.

such organizations typically operate artificial insemination units that employ highly trained professional breeders, concentrate on selection among bulls of known breeding value, and take advantage of their high reproduction rate. Through artificial insemination, one bull can be mated to several thousand females.

At the other end of the scale is the poultry breeding industry, which has only a small number of breeders. Each works with several primary breeding populations each in the order of hundreds or thousands of birds. Poultry breeding companies are usually privately owned. Their breeding procedures are generally directed by highly trained professional geneticists. The policy of most companies is not to disclose their precise breeding techniques. The multiplication of the relatively small flocks of primary breeding stocks to the hundreds of millions of commercial hybrid layers and broilers is at least partly in the hands of another type of operation: multiplier flock owners, hatcheries, and distributors. A significant aspect of this system is the separation of genetic improvement from multiplication, reproduction, and production. This dissociation has significant consequences on the character of the operations. For example, the primary breeding stock or their progeny are sometimes deliberately exposed to pathogens to allow selection for resistance. On the other hand, the stocks used to produce commercial birds are often provided maximum protection against exposure to disease so they do not transmit disease organisms to the commercial stocks.

When increased female reproduction rates become possible in sheep and cattle, as is discussed later, a shift in the character of the corresponding breeding industries could be anticipated toward today's situation in poultry. The swine breeding industry with its intermediate reproductive rate is, even today, beginning to resemble the poultry breeding industry.

ANIMAL BREEDING RESEARCH

Animal breeding research is conducted at universities, government institutions, and breeding companies or associations. The research has generally a long-term character, dictated by the generation interval of the individual domestic animal species. Experimental work is so costly that today only a few selection experiments are conducted within research establishments. The number of breeding experiments is particularly small in cattle. Therefore, field data are being used extensively for the analysis of performance of various breeds of cattle, sheep, and swine. Some in-house research, however, is also being conducted by breeding companies involved in producing and marketing breeding material for poultry and swine, as well as establishments involved in the artificial insemination of cattle.

Because of high costs, the amount of breeding research has been generally decreasing. Some administrators think a reduction is justified because sufficient new breeding methodology is already available and needs only to be applied. Another argument, particularly in poultry, is that sufficient breeding research is already being done by the breeding companies, and that these companies should assume future responsibility for breeding research. Although some research work is indeed carried out by commercial breeders, its character is mostly short term and the scope is insufficient for sustained progress. Developments in biotechnology may soon provide research administrators with another seemingly plausible justification for reducing animal breeding research. They may argue that costly breeding experiments are no longer necessary now that profound genetic changes can be introduced using the new powerful procedures that require only very few animals.

PROGRESS AND FUTURE PROSPECTS BY SPECIES AND COMMODITY

J.S. Gavora

The authors have based their discussion of the progress and changes incurred from animal breeding primarily on data from Canadian animal industries. However, in reviewing the factors that contributed to this progress, the authors have attempted to include important developments throughout the world. Today, access to the entire spectrum of new knowledge is so rapid and universal that major findings and developments can influence global production. Therefore, the prospects for the future have been discussed on a global scale.

The time frame for the review, namely the past two decades, is considered to be approximate as some data, for example on genetic gains, do not correspond exactly to that period.

DAIRY CATTLE

T.R. Batra

Various aspects of the dairy industry in Canada for 1985 are summarized from *Dairy Facts and Figures* (1985). Some 1.7 million cows were kept for dairy purposes on 67 899 farms (average 26 cows per farm). Of these farms, 44 629 commercial dairy farms reported annual gross sales of milk in excess of $5000. A total of 75 million hL of milk was produced in 1984, with total dairy revenues amounting to $3.4 billion. Of the dairy cow population, nearly 60% is bred by artificial insemination (AI) and almost 26% is enrolled in one of the federal or provincial supervised milk-recording programs (472 179). Trends in recent years have been for cow numbers and herd numbers to decline and for herd size and milk yield per cow to increase. From 1970 to 1984, annual milk yield per cow in Canada has increased from about 3345 kg to about 4680 kg (about 2.7% per year). Milk yield per cow has improved substantially during the past 15 years in herds on milk recording programs.

In the average production of all cows in Canada, much of the improvement can be attributed to production testing programs, sire and cow evaluation programs, and to making semen of proven bulls available to all dairyfarmers. Thus genetic improvement in milk production in dairy cattle results from synergistic actions of milk recording programs, AI, sire and cow evaluation, and research (Freeman 1980). With an AI population, Skjervold (1963) and Lindhe (1968) have shown that 94% of the annual genetic improvement results from the selection of sires of sons, sires of daughters, and dams of sons and that almost 70% of the progress depends on how sires are bred.

The annual rate of genetic improvement for milk yield of AI population of Holsteins in the United States over the 14 years (1961 to 1974 inclusive) has been relatively uniform (36 kg/yr) (Hintz et al. 1978). Skjervold (1963) noted that in Norway, a nationally organized program for genetic improvement of milk yield has existed for many years and that this scheme yielded a genetic gain of 1.5% per year for milk yield. In Israel over the past 23 years, annual genetic gain for milk yield has averaged 70 kg/yr (1.0–1.5%).

Yield traits

The genetic and phenotypic trends for milk and fat yield in the Canadian dairy population are summarized in Table 2. In Holsteins, the genetic and phenotypic improvements for milk production from

Table 2 Estimates of genetic and phenotypic trends in the Canadian dairy population

		Genetic trend		Phenotypic trend	
Population	Period	Milk (kg/yr)	Fat (kg/yr)	Milk (kg/yr)	Reference
Canadian Record of Performance and Dairy Herd Improvement	1965–85				Chesnais et al. (1986)
Ayrshire		37.4	–	95.4	
Guernsey		31.1	–	59.1	
Holstein		39.7	–	73.4	
Jersey		23.9	–	56.5	
Ontario Holsteins	1958–72	41.8	1.26	–	Schaeffer et al. (1976)
Quebec Holsteins	1966–72	46.3	1.07	–	Kennedy and Moxley (1975)

1965 to 1985 were about 40 and 73 kg/yr, respectively. The genetic gain represented 54% of the total improvement, which indicates that improvement from selection for milk yield has been slightly more than improvements in environment and management combined. Using the data from the national sire evaluation program in Canada, Batra (1979) estimated the genetic improvements for milk production to range from 21 to 55 kg/yr for the four dairy breeds. From reports by Schaeffer et al. (1976) and Kennedy and Moxley (1975), trends in fat and protein yield showed a similar pattern to milk yield (see Table 2). Their figures indicate that fat yield improved more rapidly than protein yield.

Product quality

Results by Kennedy and Moxley (1975) on fat and protein percentage, Schaeffer (1980) on fat percentage, and Hayes and Moxley (1980) on protein percentage have indicated a negative genetic trend in the Holstein population for these two traits. The annual rate of decline was relatively small for fat percentage averaging 0.0041%, but protein composition diminished at a more rapid rate of 0.0079% per year.

Significant improvement has been made in sanitary design, construction, and use of equipment for handling milk and its products at all steps from cow to consumer. This success has been achieved mainly through the implementation of a sanitary standard program (Heldman 1981). Progress has also been made in improving test procedures for milk quality (Marth 1981), particularly in the automation of testing (Richardson 1981).

Cost reduction

Before 1956, heifers usually did not calve until well beyond 24 months of age. Heifers within a breed appear to reach puberty at about similar weights, regardless of age (Schultz 1969, Swanson 1977). Norman et al. (1974) showed that up to 23 or 24 months of age, each month's delay in freshening increases the yield of milk at first lactation by 35 to 180 kg for Holsteins and 90 kg for Jerseys, but after 27 months of age, the yield increased only 18 kg for Holsteins and about 9 kg for Jerseys. The age at first calving has been slightly reduced in dairy heifers during the past 20 years mainly by feeding heifers better so that they reach the given weight at an earlier age. Lin and Allaire (1978) studied dairy herd improvement records in the United States and showed that Holstein cows had an average age at first calving of 30 months.

The efficiency with which the cow converts ingested feed into weight gain or milk is important in determining the productivity of dairy cattle. Freeman (1967) pointed out that efficiency of feed conversion is heritable and is correlated both phenotypically and genetically with milk production. Hooven et al. (1968) reported heritability of feed efficiency of 0.46 and its genetic correlation with milk production of 0.92, indicating that selection for milk yield would increase the genetic potential for feed efficiency.

Mortality rates of dairy calves up to 3 months of age averaged about 10% before 1960, ranging from 8 to 25% across different herds (Grunsel 1956, Oxender et al. 1973, Martin et al. 1975). During the past 20 years no change has taken place in the mortality rate of dairy calves (Speicher and Hepp 1973). The two major health problems affecting calves are diarrhea and respiratory disorders (Roy 1980).

Brucellosis has been effectively eradicated in Canada through programs involving tests, slaughter of infected individuals, and the vaccination of calves. Vaccines that increase resistance to infectious bovine rhinotracheitis, bovine viral diarrhea, and parainfluenza are used routinely. Genetic resistance to mastitis and other diseases has not yet been studied extensively. The heritability of susceptibility to mastitis is relatively low, ranging from 0.05 to 0.25 (Young et al. 1960, Wilton et al. 1972). Studies on the genetic relationship between susceptibility to mastitis and milk yield are, so far, inconclusive. Little is known about the genetic nature of resistance to other diseases in dairy cattle.

The heritabilities of calving interval, days open, dystocia, and other commonly recorded reproduction traits are less than 0.10 (Gill and Allaire 1976, Miller et al. 1967). Smith and Legates (1962) reported a genetic correlation of 0.06 between 90-day milk yield and days open. Miller et al. (1967) and Gill and Allaire (1976) also reported a positive phenotypic correlation between calving interval and milk yield. The introduction and widespread use of AI in the dairy industry has been the major factor in improving dairy cattle. Further advances will surely be made possible with improvements in multiple-ovulation and embryo transfer techniques.

Future prospects

Research, development, and use of improved techniques for animal breeding during the past two decades have given good results. However, optimum rates of improvement in production traits are not yet being achieved. New technology and methods are being researched and developed for increasing the genetic improvement in dairy cattle. Genetic engineering, biophysical profiling, embryo manipulation, and crossbreeding are techniques that may contribute to the future improvement of dairy cattle.

Continued efforts will be needed to obtain further improvement in procedures for sire and cow evaluation. In particular, there is a need to increase the number of traits for which dairy animals will be evaluated and means by which to quantify correlated responses to selection for milk production and other economically important traits.

BEEF CATTLE

J. Wilton

Canada's beef output in 1985 was about 945 700 tonnes on a carcass basis (Agriculture Canada 1986). Some 75% of this output was from market steers and heifers and, consequently, was valued at $290/100 kg (Agriculture Canada 1983). The remaining 25% consisted mostly of cull cows, valued at about $180/100 kg. Total value of beef output was therefore about $2480 million.

Canada's beef cattle population in 1986 was 3.04 million cows, 1.27 million steers, 0.23 million bulls, and 1.23 million heifers (Agriculture Canada 1986). Therefore, small genetic changes on an individual animal basis can have a very large effect nationally when introduced to the whole population.

Yield traits

Changes have been made in yield traits through breed substitution, multiple gene effects, and single gene effects.

Breed substitution Substitution has played a major role in changing beef production in Canada in the past two decades. Large numbers of cattle of several breeds have been imported from Europe and multiplied in Canada since the late 1960s and early 1970s. The number of new animals registered in the breed association in 1985 for several breeds showed the traditional Angus, Hereford, and Shorthorn at 15 000, 43 000, and 3000, respectively, and the imported Charolais and Simmental at 20 000 and 19 000, respectively. Commercially, the effect of these numbers has been even more substantial as sires from these imported breeds are used in crossbreeding programs.

Differences in yield traits between breeds have been studied in detail. Koch et al. (1976, 1979, 1983) and Rahnefeld et al. (1983) showed major differences in weight among different breeds and crosses. Koch et al. (1979) showed differences in carcass weight from 251 to 384 kg for Hereford–Angus crosses to Chianina–Hereford crosses, for animals marketed at equal levels of fatness. These differences have prompted the use of sires of breeds producing heavier carcasses in crossbreeding programs. Their use offers considerable scope for changes in average weights of carcasses marketed in future. The heritability of carcass weight and retail yield weight has been found to be high, namely 0.58 (Koch et al. 1982).

The genetic changes that are expected with such high levels of heritability have in fact been calculated. The best estimates available in Canada are those evaluated in the Canadian beef sire monitoring program (Agriculture Canada 1986). The average genetic merits of bulls of several breeds from 1973 to 1985 are shown in Table 3. Gain

Table 3 Changes in mean estimated breeding values of progeny of sires evaluated in the Canadian beef sire monitoring program[1]

Year	Angus	Charolais	Hereford	Simmental
	Weight gain from birth to one year of age, (kg)			
1973	0	0	0	0
1977	5.3	0.3	2.3	2.5
1981	10.5	3.0	9.9	5.0
1985	19.0	5.4	17.2	10.6
	Ease of calving (points)[2]			
1973	0	0	0	0
1977	0	1.5	0.1	0
1981	−0.1	1.3	0.1	0.4
1985	−0.4	1.2	−0.8	0.3

[1] Source: after Agriculture Canada (1986).

[2] Calving ease scored from 0 for surgery required, to 50 for assistance, to 100 for no assistance.

to one year of age is closely related to yearling weight and, hence, to carcass and retail-yield weights. A definite positive trend over time has been shown for the Angus and Hereford breeds. Angus sires evaluated in 1985 will sire calves 19.0 kg heavier at one year of age than would sires evaluated in 1973. The trend is not as pronounced in the Charolais and Simmental breeds, in which more emphasis has been placed on improving calving ease.

Multiple gene effects The effects associated with heterosis have not been considered to be as important as breed differences in crossbreeding to change the weight of the product. However, they do have some importance as indicated by estimates of 10 and 6% for direct and maternal heterosis in carcass weight, respectively (Koch et al. 1983).

Single gene effects Few single gene effects influencing weights of animals have yet been identified. The major genes that have been studied are those controlling dwarfism. The snorter dwarf condition, inherited as a simple recessive gene, and the compressed dwarf condition have been identified as problems. Both are characterized by small size as well as a variety of other characteristics (Warwick and Legates 1979).

Product quality

The first major factor determining product quality is carcass composition. The relative weights of fat, lean, and bone that make up the total weight of the carcass greatly influence its economic value. In Canada, beef carcasses are classified by grade which is determined primarily by youthfulness. Most carcasses are classified as grade A. This grade is subdivided into grades A1 to A4 on the basis of fatness. Carcasses graded A1 have less fat than those in the other grades (Table 4) (Fredeen et al. 1981). The percentage of the marketing that each of these categories constitutes has changed considerably from 1972 to 1981, as shown by Agriculture Canada market reports. As a result, fat in carcasses being marketed has decreased from 22 to 20% (Table 5). This decrease is substantial in view of the concomitant increase in carcass weights.

The extent to which the phenotypic trends just described result from genetic or environmental effects has not yet been determined. Part of this trend probably results from genetic differences, because of the extent to which different breeds have been used in crossbreeding programs. For example, Koch et al. (1976, 1979) and Berg et al. (1978) have shown that different breeds of sire produce large differences in fat percentage at a given weight of carcass.

Besides the use of different breeds, selection of animals within a breed to bring about changes in weight at one year of age brings correlated changes in fatness at a given weight of carcass (Koch 1978, Koch et al. 1982). Koch et al. (1982) found percentage of fat in the retail product at a constant age to have a heritability of 0.63. Selection for reduced subcutaneous fatness, a trait measured in many current bull-testing programs for beef cattle, would have the desirable

Table 4 Changes in grades of beef marketed in the A grade[1]

		Marketed beef	
Grade	Fat[2] (%)	1972 (%)	1981 (%)
A1	19.0	33.5	56.8
A2	22.4	42.0	35.1
A3	25.6	18.0	6.7
A4	28.3	6.5	1.4

[1] Source: Livestock Market Review. Agriculture Canada (1972, 1981).

[2] Source: Fredeen et al. (1981).

Table 5 Changes in beef carcass characteristics, 1972–1981[1]

Characteristic	1972	1981
Carcass weight (kg)	260	271
Chemical fat (%)	22.2	20.8

[1] Based on the sources in Table 4.

effect of reducing fatness and increasing the percentage of retail yield at either a constant weight or age.

Muscle weights relative to weight of bone also differ between breeds (Berg and Butterfield 1976, Berg and Walters 1983). Changes in muscle weight relative to amount of bone can also be influenced by the gene for double muscling (Warwick and Legates 1979). This condition is inherited as a simple recessive, although its expression is modified by many other genes that affect the degree of muscling. Double-muscled animals have an increased number of muscle fibers in each muscle and have a higher ratio of muscle to bone than normal animals. To date, selection has mostly favored the reduction of double muscling because of the calving difficulties associated with double muscling. Increasing the frequency of the double-muscling gene has considerable potential if these associated reproductive problems can be overcome.

The distribution of lean, fat, and bone in various cuts of the carcass is the second determinant of quality in the product. Berg and Walters (1983) reviewed extensively the development of fat, lean, and bone and the factors determining their distribution. Genetic differences in muscle distribution between breeds appear to be small, whereas those in fat distribution appear to be more important. The ratio of subcutaneous fat to intermuscular fat has been shown to differ between breeds. The size of these differences depends on the stage of maturity at which the comparisons are made. The use of breeds that fatten at an older age, such as the Charolais, in crossbreeding may have resulted in a change in distribution of fat, but these changes have not yet been documented.

The heritability of distribution of fat and bone within breed has not yet been examined. Koch et al. (1982) found the heritabilities of percentage of kidney fat (a measure of internal fat) to be high at a constant age, but this trait may reflect a tendency either to fatten or to deposit fat in one place relative to another.

The third determinant of product quality is palatability. Measurements of tenderness and flavor are important indicators. Koch et al. (1979) concluded that differences in meat palatability among breeds, as measured by a taste panel, were small among animals of similar age. They found tenderness, as measured by shear scores, differed only slightly.

Koch et al. (1982) found the heritability of shear score to be moderate, with a value of 0.31. Selection may be useful in the future, but genetic changes to date have likely been negligible.

Cost reduction

A major factor in reducing cost of production is reproductive rate. Crossbreeding programs have been used increasingly in industry, although exact numbers concerning the extent of crossbreeding are not available. The increase from heterosis in number of calves weaned per cow bred has been well documented (Warwick and Legates 1979). This increase results from both the cow and the calf being crossbred. The influence of breed differences in reproductive rates appears to be small. Lawson et al. (1980), for example, found no differences in conception rates or services per conception among breed crosses of cows. Selection for conception rates is not considered to be an effective method of improvement because of the low heritability of this trait. Selection for ease of calving, which Laster and Gregory (1973) showed to be correlated to survival rates of calves and which is economically important itself, should prove more effective in improving reproductive rate because it has a moderate level of heritability (Tong et al. 1976). Genetic trends have in fact been found (see Table 3) in the Charolais breed, whose breeders have emphasized this trait using sires evaluated on the records of their progeny. The number of calves born alive and surviving to weaning has been increased also through single gene effects, by reducing frequency of abnormal calves with bulldog and crippled calf syndrome.

Another important factor in cost of production is feed efficiency. The increase in numbers of producers using crossbreeding programs has had a desirable effect in this area as well, although the extent of these changes has not yet been documented. The changes in efficiency of production do not result from heterosis in this case, as heterosis estimates are generally low (Warwick and Legates 1979). Rather, changes in efficiency are more likely to stem from the use of specialized sire and dam lines, as shown in the modeling work of Wilton and Morris (1976). The matching of genotype with environment is an important part of the use of crossbreds as shown by Fredeen et al. (1982*a*,*b*).

Selection for efficient feed conversion should prove effective, as shown by the estimates reviewed by Preston and Willis (1974). However, few measurements of feed intake are currently being taken in performance testing programs for beef cattle. Most changes that have taken place to date would result from the genetic correlation of feed conversion with gain, which Preston and Willis (1974) reviewed as being -0.3 to -0.8. Newer methods of measuring feed intake with electronic equipment offer the potential for direct selection for feed conversion efficiency in future.

Future prospects

The performance of beef cattle continues to improve as a result of selection for traits that increase yield of beef and improve product quality and that reduce costs. The numbers of animals on which performance data are recorded could be increased by the use of microcomputers on farms. One challenge in the future will be to integrate data from on-farm microcomputers with central data bases, from which estimates of breeding values for a variety of traits could be obtained. The number of traits that are evaluated could also be increased. For example, an evaluation of sires for maternal abilities of their daughters could be included. New electronic equipment for measuring feed intake offers the potential for direct selection for this trait in future, in contrast to the present method, which relies on correlated responses with selection for growth. Similarly, new equipment for measuring subcutaneous fatness of animals offers the potential for increased selection pressure for composition of gain.

Continuing refinements in crossbreeding programs are likely to take place. Major efforts will be made in the matching of specific breeds and combinations of breeds with specific management programs. New techniques in embryo transfer make it possible to obtain embryos specialized for market traits which would result in a greater use of specialized sire embryo and dam lines. This specialization can be further exploited by the use of twinning with specialized embryos, which would also be of major importance in dealing with the low rate of reproduction in beef (Reid et al. 1986).

Long-term developments are possible by using single gene effects. Traits such as ovulation rate, growth hormone production rate, and muscular hypertrophy may well be altered. More research is required on the interaction of such changes with other characteristics. Much more work is also required on control mechanisms and locations of genetic coding on chromosomes before attempting specific gene manipulation.

SHEEP

J.N.B. Shrestha

Since the first sheep were imported from France in about 1650, the Canadian sheep industry has played an important role in providing food and wool throughout agricultural Canada until the 1950s (Slen 1954). Low world prices for wool after the second world war brought changes to the sheep industry not only in Canada but also in leading wool-producing nations. In Canada, the sheep population declined from an all-time high of 3.6 million in 1931 to a record low of 0.6 million in 1977, which represented an 85% loss in total numbers. From 1977 to 1985, the sheep population has increased again by 34%. The fall in production of Canadian lamb and mutton from 32 311 tonnes in 1946 to 8560 tonnes in 1985 resulted in imports increasing from 4.5 tonnes in 1948 to 11 737 tonnes in 1985, which account for 60% of the country's requirement. Domestic consumption of lamb and mutton has gradually declined from 3.4 kg a person in 1923 to 0.8 kg in 1985. In recent years, wool, lamb, and mutton have not been a major source of income for Canadian farmers; the total cash receipts from the sale of lamb and mutton now represent less than 0.5% of the total red meat consumed, and the importance of lamb and mutton relative to other sources of meat continues to decline. The total value of wool, lamb, and sheep was $82 million in 1985, which represented 1% of livestock products in Canada.

Genetic improvement in sheep is complicated by changing economic and social conditions and is characterized by large differences among farmers in feed, climate, housing, and breeds. Similarly the relative economic value of products, namely meat, wool, milk, and skin, has changed with time. Over the last 35 years, the primary product of the Canadian sheep industry has shifted from wool to meat. When wool prices plunged to an all-time low, sheep producers found themselves in the difficult position of having to pay more for shearing the fleeces than was the actual value of the product.

Rapid advances in sheep breeding during the past two decades have been achieved by using available scientific knowledge to develop effective breeding methods that improve economically important traits.

Genetic improvement programs using various schemes for the recording and testing of performance have been introduced in several countries throughout the world (Owen 1971, Clarke and Rae 1977, Tomes et al. 1979, Croston et al. 1980, Shrestha et al. 1982). In Canada, a new technology for a highly automated, accelerated, and programmed system of lamb production has now been developed. Its use allows lamb production per ewe to be doubled or tripled through intensive management practices, without apparent detrimental effect on the health and performance of sheep (Heaney et al. 1980, Ainsworth et al. 1986).

Yield traits

Most estimates of genetic parameters for sheep are sufficiently high to allow response to selection (Terrill 1962, Turner and Young 1969, Rae 1982, Shrestha and Heaney 1985, Shrestha et al. 1985, 1986*b*). Estimation of genetic and phenotypic parameters for economically important traits after adjustment for environmental factors has resulted in the construction and application of selection indexes (Clarke and Rae 1977, Ponzoni 1979). Selection experiments have demonstrated that effective genetic change has been achieved from artificial selection with single or multiple traits.

Eight generations (23 years) of selection for increased weight of clean fleece have been successful in increasing wool production by about 20% (0.9% per year) at the Trangie Agricultural Research Station, Australia (McGuirk and Atkins 1979). Although considerable year-to-year fluctuations in relative performance caused difficulty in assessment, McGuirk and Atkins concluded that genetic response was at a slower rate in the later years compared to that achieved in the earlier years. Correlated responses were similar to those predicted. Adult greasy fleece increased by 7.7% (0.16 kg per head) as a result of 10% improvement in clean fleece weight. Also, a reduction of 32% in crimp frequency (3.31 vs. 4.33 crimps per centimetre) and an increase of 7% in average fiber diameter (21.2 vs. 19.9 µm) resulted from correlated response to selection. In another study, increasing the yield of clean fleece was shown to increase the danger of fleece rot, weathering, and dust penetration (Barlow 1974).

Lax et al. (1979) compared single-trait selection with selection using a two-trait index in Hampshire sheep. The traits studied were 90-day weight and backfat probe at the seventh rib as a measure of fatness. Over 5 years, selection in the weight-selected line was effective in increasing the 90-day weight by 0.62 kg/yr, with correlated increases of 0.04 cm in backfat at the seventh rib and 0.05 unit in the index, which measured the combined value of both traits. Selection in the backfat-selected line decreased backfat by 0.03 cm/yr with essentially no change in weight and an increase of 0.07 unit in the index. Index selection increased the 90-day weight by 0.33 kg/yr, decreased the backfat probe measurement by 0.02 cm/yr, and increased the index by 0.1 unit per year.

Crossbreeding has played a key role in exploitation of breed differences as a method of genetic improvement in sheep. In Canada, extensive crossbreeding studies were conducted by Vesely and Peters (1979, 1981), who compared lamb production of pure breeds with their two-, three-, and four-breed crosses. These studies demonstrated the superiority of crossbreds over purebreds in growth, survival, and reproduction.

Important effects of heterosis, breed, and general and specific combining ability on ewe productivity have been reported (Shrestha et al. 1983). Therefore, both additive and nonadditive effects should be considered in developing breeding strategies that maximize productivity for commercial lamb production.

Product quality

An effective sheep breeding program in Norway used a selection index based on carcass weight, carcass quality, and fleece weight for rams and resulted in an estimated overall genetic progress of

1.0–1.3% per year (Eikje 1975). Also, weaning weight showed a genetic gain of about 0.25 kg/yr. Genetic gains in carcass weight, hindquarter weight, and loin-eye area were estimated at 0.24 kg, 0.09 kg, and 0.22 cm^2, respectively. Annual genetic loss as a consequence of correlated response to the selection was 0.03 unit for carcass grade, 0.01 kg for weight of kidney and kidney fat, and 0.02 kg for fleece weight.

Most of the published genetic parameters for lamb carcass traits are preliminary estimates because of the small sample sizes involved. Recently, Wolf (1982) reported heritability estimates for proportions of lean tissue that ranged from 0.07 to 0.65, indicating that selection may be effective in changing lean distribution. However, where heritability estimates were highest, the coefficients of variation were low, thus reducing prospects for rapid progress. Wolf (1982) also estimated a positive genetic correlation of 0.17 for the relationship between average daily gain from birth to slaughter and the proportion of total lean in the higher-priced cuts. Shrestha et al. (1986*a*) reported heritability estimates from 0.38 to 0.67 for shoulder and leg (trimmed and lean), total trimmed retail cuts, total lean, chilled carcass weight, and lean weight gain per day. Estimates based on loin, rack, front, back, total retail cuts, kidney fat weight, dressing percentage, and chilled carcass weight gain per day showed lower and nonsignificant relationships with total trimmed retail cuts or total lean. Selection for better lean distribution in any one of the highly heritable, higher-priced cuts might have a correlated response in the overall lean distribution. The development of accurate ways to measure carcass quality in live animals (Bass et al. 1982) could reduce the cost of selection for total lean. Bradford (1967) emphasized the practical value of developing such methods. He stressed that industry was far more likely to take and use measurements of carcass quality on live animals than to use even the best progeny testing scheme for carcass quality. The existing pattern of market lamb production, in which certain meat-type breeds are used as sire breeds for crossing, offers a means for improving carcass quality. To achieve an improvement, increased quality selection efforts can be concentrated on sire breeds that form only a small proportion of the total population.

Cost reduction

The important traits for reducing costs in sheep production are growth rate, lean muscle yield, age at sexual maturity, reproductive performance, feed efficiency, and viability. Although some information on growth rate, age at sexual maturity, and reproductive performance is available, data on lean-muscle yield, feed efficiency, and viability are limited.

In ewe lambs, a distinction must be made between puberty and sexual maturity, because ewes do not attain their full reproductive capacity until they become adult. No studies on genetic change from selection for early puberty and sexual maturity in sheep were found in the literature. Although fecundity in younger sheep is lower than in mature ones, breeding lambs at 6 months of age could reduce the generation interval and permit progeny testing at an earlier age.

In certain breeds, saving offspring from ewe lambs that breed early seems to result in selection for early sexual maturity and greater fertility (Mair 1963). Females of highly prolific breeds, such as Finnish Landrace (Maijala and Osterberg 1977) and Romanov (Ricordeau et al. 1978), experience their first estrus at a relatively early age. There is some evidence that early breeding may result in enhanced subsequent fertility and an increase in the lifetime productivity of the ewe (Baker et al. 1978). Recently, plasma hormonal levels and testis growth in rams have been studied, as possible indicators of age at puberty and ovulation rate in siblings or offspring (Land 1973, Bindon and Piper 1979). These traits may be used as additional selection criteria for reproductive performance.

Selection for fleece weight has generally shown no correlated changes in reproductive rate of the Australian Merino (Turner 1977). But McGuirk and Atkins (1979) found that selection for increased fleece weight reduced the number of lambs born per ewe joined by increasing the proportion of dry ewes. These authors also reported that the incidence of dry ewes was heritable. In the New Zealand Romney, selection for high twinning rate led to slightly lower fleece production (Clarke 1972). Testis growth may be used as a criterion for genetically improving both the male and female reproductive rates (Land 1973, 1977*b*) because the same gonadotrophic hormones are involved in the physiological control of reproductive activity in both sexes. Reported evidence suggests a genetic relationship between testis growth in rams and ovarian activity in ewes (Land 1973, Land and Carr 1975, Land and Lee 1976). Despite earlier evidence that genetic improvement of reproductive rate is slow (Turner 1969), high heritability estimates have been reported for testicular measurements in sheep (Hanrahan and Quirke 1977, Thorsteinsson et al. 1982).

Selection for increased fleece weight did not influence body weight, and pen feeding studies showed that the increased fleece weight did not result from increased feed consumption (Williams and Winston 1965).

Although the cost of importing and testing exotic breeds is usually high, the potential benefits often justify the investment. Dickerson (1977), in a study of crossbreeding of Finnsheep with other breeds, concluded that Finnsheep crosses with such breeds as Dorset, Suffolk, Targhee, or Rambouillet, when used as commercial ewes to be mated with meat-breed sires, can reduce ewe cost per kilogram of market lamb by 20 to 25%. Crossbred ewes that are 25% Finnsheep (instead of 50%) produce about 20 more lambs born alive per 100 ewes than domestic crossbred ewes. Under poor range conditions and with severe climatic exposure at lambing, the 25% Finnsheep ewes may raise nearly as many lambs as the 50% Finnsheep ewes and have a longer productive life.

The high prolificacy of the Booroola Merino is associated with a major gene affecting ovulation rate (Piper and Bindon 1982). By using genetic segregation of the major gene to control fecundity, predetermined proportions of Booroola Merino in crosses with domestic breeds could have a major role in increasing ewe productivity. The Texel breed of sheep from Holland excels in meat quality (Wolf et al. 1980) and displays a potential for efficient production of heavy and lean carcasses when used as the sire breed for the production of market lambs. It may be a valuable breed to introduce to Canada.

Future prospects

The overall economic efficiency of commercial lamb production could be improved in the future by assembling potential sources of both domestic and exotic germplasm into new breeds or by using appropriate crossbreeding systems. The improvement of established breeds through introduction of exotic breeds that have demonstrated superiority in some important production traits could result in rapid genetic gains.

The Canadian Record of Performance (ROP) program for sheep (Shrestha et al. 1982) implemented in 1976 was intended to provide sheep breeders with a simple means of measuring and recording performance on the farm for use in the genetic improvement of their breeding stock. The number of sheep breeders participating in the program has increased dramatically over the first 6 years. This program has the potential to stimulate genetic change in the national flock.

The conventional system of lamb production will likely continue to be used by Canadian farmers on marginal and submarginal agricultural lands. However, in areas closer to centers of population, intensive production systems based on housed sheep will continue to be developed. Intensive sheep production systems under controlled environment (Ainsworth et al. 1986) would be made even more feasible if lambing frequency could be increased from three lamb crops in 2 years to two lamb crops a year without any additional capital layout for buildings and equipment. This increase has yet to be proven possible. Combined with larger litter size and improved survival rates, the intensive production of sheep has the potential of achieving five lambs per pregnancy with a mean lambing interval of 6 months. This potential increase in productivity will encourage the implementation of the new technology that could make intensive production of lambs from housed sheep possible. Dramatic progress may be achieved even more quickly by using genetic engineering approaches that are discussed later.

Thus, genetic improvement could be accelerated by improving the accuracy of assessing the genetic potential of breeding stock for selection and synthesis of new breeds with a combination of economically important traits to meet the challenges of the future.

SWINE

M.H. Fahmy

In 1984, the Canadian swine industry accounted for $1.7 billion (about 9.1%) of the total farm cash receipts, with nearly 11 million pigs on about 56 000 Canadian farms. For some provinces such as Quebec, that contribution was as high as 20%. In that year, Canada exported about 173 000 tonnes of pork, which represented about 20% of its swine production, compared with only 5% in 1969.

Over the past two decades, annual commercial slaughter almost doubled, rising from 7.8 to 14.6 million pigs. The increased popularity of swine breeding in Canada may be attributed in part to the improved profitability of the operation through better returns and lower production costs.

Canadian and foreign research in the field of quantitative genetics has resulted in better use of genetic theories in practical swine production. Recent developments, such as the use of marker genes and hormonal profiles in selecting for economically important traits, as well as application of new techniques, such as the use of ultrasonic equipment to evaluate carcass quality and laparoscopy to determine ovulation rate, have also contributed to the improvement in swine production.

Yield traits

The main component traits of yield are fertility, prolificacy, and pre- and post-weaning growth rate of piglets.

Yield is often measured in terms of kilograms of trimmed pork marketed at 95 kg live weight. Quebec has been one of the first provinces in Canada to initiate an on-farm ROP program for sows. The results obtained after 6 years on this program are presented in Table 6. They show a continued improvement in productivity of the sow in all aspects related to reproduction. The proportion of this improvement attributable to genetic change is yet to be determined.

Experimental studies to improve ovulation rate and litter size by selection showed that whereas ovulation rate responds to direct (Cunningham et al. 1979) and indirect selection (Ollivier and Bolet 1981), litter size showed no corresponding improvement. The heritability of ovulation rate was found to be of moderate magnitude, about 0.4, (Cunningham et al. 1979). On the other hand, the genetic

Table 6 Changes in performance of sows on Quebec swine farms, 1980–1986

	Performance						
Traits	1980	1981	1982	1983	1984	1985	1986
Interval, weaning–conception (days)	28.1	23.3	17.1	12.7	12.1	11.3	10.8
Number of pigs born alive per litter	9.5	9.6	9.7	9.8	9.8	9.9	10.0
Number of pigs weaned per litter	7.7	8.0	8.2	8.3	8.3	8.4	8.4
Number of litters per sow per year	–	1.4	1.6	1.8	1.8	1.9	1.9
Productivity per sow per year (pigs)	10.8	11.5	13.4	14.8	15.2	16.0	15.9

Source: after Anonymous (1986).

component of litter size is generally low, only 5–10% (Strange and Smith 1979), probably because of negative maternal effects (Revelle and Robison 1973). Therefore, direct selection for increased litter size was not effective. A feasible alternative is to select for high ovulation rate and to develop methods and techniques to reduce pre- and post-natal mortality.

Legault and Gruand (1976) proposed that, with the many data accumulated from national recording programs, a small number of sows with extremely high reproductive performance could be identified and selected. The genes from these highly prolific sows could then be concentrated by using their sons in successive matings to other highly prolific sows. Two studies in France (Legault et al. 1981) and in Britain (Bichard and Seidel 1982) test this approach. Preliminary results from the French work showed that, although the ovulation rate of the highly prolific sows was significantly higher than in the control lines, the number of live embryos at 30 days of gestation was similar in the two lines because of higher embryonic loss.

Dufour and Fahmy (1975) showed that crossbred embryos had a better chance of survival than purebred ones. Crossbreeding, therefore, is an effective means for increasing litter size. Johnson (1981), summarizing North American crossbreeding studies reported since 1970, showed that crossbreeding had the greatest effect on the survival of the piglets after farrowing. Crossbreeding studies also showed that the size and weight of litters are higher for crossbred sows than for purebred sows (Table 7). Johnson (1981) found that pigs weaned from crossbred sows at 2 days weighed 6.4 kg more than did those from purebred sows. These results confirmed those of Sellier (1976) who found an 8.0-kg improvement in weaned piglets from crossbred sows at 21 days. These figures represent almost 10 and 17% improvement, respectively, over the purebreds.

Because the heterosis observed is often proportional to the degree of diversity in performance between breeds, different genetic resources can be useful in crossbreeding programs. Chinese breeds of pigs were reported as being extremely prolific: the Taihu, Minpig, Xinhui, and Large Spot sows farrow litters of 16.1, 15.3, 13.3, and 13.3 pigs and wean litters of 12.0, 10.6, 10.2, and 11.7 pigs, respectively (Wu and Zhang 1982). These breeds are also characterized by a high number of functioning teats (about 16), but unfortunately the piglets have a slow growth rate and, when fed to slaughter weights, become unacceptably fat by Western standards. Thong (1974) reported on another prolific breed from Southeast Asia, the Vietnamese breed I, which may potentially also contribute genes for prolificacy.

Recently, France became the first Western country to import the Chinese breeds Meishan, Jiaxing, and Jinhua and to use them in crossing with Large White and French Landrace (Legault and Caritez

Table 7 Average individual and maternal heterosis from crossbreeding studies in swine

	Individual heterosis		Maternal heterosis	
	Sellier (1976)	Johnson (1981)	Sellier (1976)	Johnson (1981)
Litter size at birth (no.)	0.30 (3.0%)	0.23 (2.4%)	0.75 (8.0%)	0.93 (9.9%)
Litter size at 21 days (no.)	0.45 (6.0%)	0.70 (10.2%)	0.85 (11.0%)	0.93 (13.0%)
Litter weight at 21 days (kg)	9.00 (12.0%)	4.20 (12.0%)	8.0 (10.0%)	6.40 (16.7%)

Source: from Johnson (1981).

1983). Preliminary results from the French trials indicated that certain crosses between Chinese and European breeds resulted in a crossbred sow that had its first farrowing at least 1 month earlier, was more efficient in feed conversion, and produced from five to eight more weaned piglets than pure European breeds.

In 1973, the national average daily gain, as determined through tests of progeny from tested sires in Canadian ROP stations, was 794 g; 10 years later it was 880 g. There has, therefore, been an average yearly phenotypic improvement of about 8 g. In a Landrace population selected for post-weaning average daily gain during eight generations and using a Yorkshire population as a control, Rahnefeld (1971) reported a genetic improvement of 8.2 g per generation.

Numerous selection experiments used indices combining growth rate with other traits, particularly backfat thickness (MacIver 1971, Fredeen 1976, Ollivier 1979, Vangen 1979, Mikami 1982). Ollivier (1980), after 11 years of boar selection for an index that combined average daily gain of males and females, reported improvements of 12 g for males and 6 g for females annually. On the other hand, Vangen (1979), after 12 years of divergent selection using a similar index, reported a slightly increased growth rate in the line selected for high index and almost no change in the line selected for low index. Nonconclusive results were reported by Mikami (1982) who selected seven strains of swine according to an index that included backfat thickness, loin-eye area, and percentage of ham in the carcass, as well as average daily gain. Although the response to selection in the first three traits was positive, the response in average gain was low or without trend, except for one strain in which it was significant. Dettmers et al. (1965), selecting for a reduction in size of pigs at 140 days, reported a decline of 29% over 11 years.

Studies on the effect of crossbreeding on growth rate were reviewed by Johnson (1981). He calculated the average individual heterosis in daily gain at 8.8% for studies conducted in North America, which compares well with the 6% estimate reported by Sellier (1976) for the European studies. In both reviews the maternal heterosis for average daily gain was very small suggesting that maternal effects are unimportant beyond weaning.

Product quality

In swine, the main objective is to produce high-quality carcasses with low fat and high lean content and freedom from odors. As shown from Canadian ROP statistics, between 1973 and 1983 the average backfat thickness of Canadian hogs was reduced from 19 mm to 14 mm, a phenotypic decline of about 0.6 mm/yr. Because backfat thickness was found to be highly correlated with carcass leanness and because it is easy to measure, it has been used widely in national swine improvement programs and in many selection experiments. It was also included in selection indices, with growth rate (MacIver

1971, Vogeli 1978, Vangen 1979, Ollivier 1980) and feed conversion (Webb and King 1976), carcass length, and loin-eye area (Bernard and Fahmy 1970). These experiments indicated that a positive though moderate response to selection can be achieved (Table 8) and that the correlated responses in the other carcass and reproductive traits were favorable.

During the past two decades, efforts to increase leanness shifted from indirect selection, through selecting for thinner backfat, to direct selection for leanness using ultrasonic techniques that measure the depth or cross section of *Musculus longissimus dorsi*. Leymaster et al. (1979) showed that a slight response was achieved after four generations of such selection (see Table 8).

A new approach to the improvement of meat quality by selection using genetic markers has been developed in Denmark (Andresen and Jensen 1979, Andresen et al. 1979). They reported that selection based on the H blood group system alone or in conjunction with phosphohexase isomerase was more effective than selection based directly on meat quality.

Smith and Webb (1981) demonstrated methods for the identification of a major gene in a quantitative trait, as well as the techniques for using such genes in breeding strategies. This approach has been successfully applied, for example, to the elucidation of the gene for halothane reaction in pigs, which indicates susceptibility to the porcine stress syndrome (Eikelenboom and Minkema 1974). From the mid-1970s, great attention has been given to the porcine stress syndrome, a range of symptoms associated with the high liability to develop pale, soft, and exudative meat and sudden death of susceptible animals in response to stress. Webb et al. (1982) reported that the halothane test performed on pigs between 6 and 15 weeks of age accurately identifies susceptible animals, that breeds differ in the percentage of animals susceptible, and that this trait is based on a single recessive gene. Carriers can now be identified by this test and, thus, can be prevented from mating.

Renard et al. (1982) studied the association between the swine histocompatibility system (SLA) and production traits of French breeds. The performance level of several economically important traits in swine was found to be associated with the SLA haplotype.

Studies to solve the problems of sex odor in boars have been reported recently. Willeke and Pirchner (1982) showed that five generations of selection for and against 5α-androsterone, the steroid responsible for sex odor, were effective in changing its level. However, they also reported significant correlated responses in carcass traits to selection for the steroid.

Because carcass quality traits show very little heterosis (Young et al. 1976), the carcass merit of crossbred pigs can be reasonably predicted from the average of the two purebreds involved in the cross. The present trend is to use sire breeds known for their superior carcass quality, such as the Hampshire and Duroc in North America and the Pietrain in Europe, to mate with breeds or crosses noted for their superior prolificacy and mothering ability, such as the Yorkshire (Large White), Landrace, or Lacombe or their crosses. This concept of specialized sire and dam lines has been gaining much attention recently. Efforts are continuing in Britain to develop a special sire line using the concept of open migration (Webb and King 1976).

Table 8 Results from some selection studies to improve carcass quality and feed efficiency in swine

	Changes per generation		
Traits selected	mean	(%)	Reference
Backfat thickness (mm)	–1.2	3.2	Hetzer and Harvey
	–0.9	2.8	(1967)
Backfat thickness (mm)	–1.2	4.0	Gray et al. (1968)
Backfat thickness (mm)	–0.6	2.6	Berruecos et al. (1970)
Carcass length (mm)	+6.1	0.5	Duckworth and Holmes (1968)
Lean (%)	+0.38	0.6	Leymaster et al.
Weight of lean (kg)	+0.50	1.6	(1979)
Backfat + Length (mm)	–2.2	7.3	Webb and King
Backfat (mm)	M*–0.5	3.0	(1976)
	F*–0.5	2.6	
Index growth rate (g)	M 14	1.9	
	F 41	6.3	
Feed efficiency	M –0.04	1.2	
	F –0.07	2.0	
Feed efficiency	9	0.2	Bernard and Fahmy (1970)
Carcass score (pts)	0.7	1.1	
Feed efficiency	0.2	0.6	Junst et al. (1981)

*M = males; F = females.

Cost reduction

Between 1973 and 1982, feed efficiency of the boars on Canadian test stations improved from 3.03 kg to 2.44 kg of feed per kilogram of gain, an annual phenotypic improvement of about 65 g/kg. Thus, on average, a pig requires 60 kg less feed now to reach market weight than it did 10 years earlier. Direct selection for feed efficiency was reported by Bernard and Fahmy (1970) and Junst et al. (1981). In both studies the genetic response to selection was rather low, (0.09 and 0.10 kg feed per kilogram of gain, respectively (see Table 8)). On the other hand, Vangen (1979) and Sather and Fredeen (1978) selected swine on the basis of an index that included growth rate and backfat thickness; they reported a substantial improvement in the two traits and showed a marked, correlated improvement in feed efficiency. Therefore, it may be economically more advantageous to select indirectly for this trait as it is expensive to measure. Feed efficiency is among the traits that show moderate heterosis (Sellier 1970, Johnson 1981).

Controlling embryonic and postnatal mortality seems to be most important in improving pig production by reduction of production costs. Up to 30% of embryos die before farrowing (Dufour and Fahmy 1975, Marlowe and Smith 1971) and another 20 to 25% of piglets die before weaning (Fahmy and Bernard 1971, Backestrom 1973). Much research has been conducted to relate embryonic mortality to uterine capacity (Dziuk 1968, Bazer et al. 1969, Fenton et al. 1972, Webel and Dziuk 1974). Up until 30 days of pregnancy, uterine space seems to have little effect on embryo survival, but crowding can be a limiting factor during the later stages of pregnancy. The causes of embryonic mortality during the first stages of pregnancy still mystify scientists. A crossbred embryo has a better chance of survival compared with a purebred one (Dufour and Fahmy 1975). This finding indicates that mortality may constitute natural selection against genetically less fit embryos.

Bereskin et al. (1973), reporting results on over 10 000 litters, showed that only 72% of the pigs born alive survived to weaning and 66% survived to market weight. Although much of this loss can be attributed to inadequate management, many studies have tried to relate mortality to measurable factors. Stanton and Carroll (1974) reviewed the literature on piglet perinatal mortality and compared it to that of other species. They showed that many characteristics of the sow, such as uterine blood flow, psychological stress, and endocrine factors, can influence the embryonic and postnatal mortality of the piglets. They also stated that more research is needed on the physiological consequences of psychosocial stress in the pregnant sow.

In an attempt to improve piglet survival rates by genetic means, Fahmy and Bernard (1978) selected Yorkshire swine for their level of hemoglobin at 28 days of age to develop an anemia-resistant line. After four generations of selection a marked and highly significant difference in hemoglobin level was observed between the selected and control lines in the piglets up to 28 days of age (8 vs. 6.5 g/100 mL). They concluded that pigs with a naturally high concentration of iron or with a better iron metabolism might be developed; such piglets would be better able to maintain an adequate hemoglobin level and would have a higher rate of survival.

Recently, several attempts have been made to understand and control disease resistance in swine. For example, in Canada, genetic aspects of atrophic rhinitis, a viral disease that causes slower growth rate and reduced efficiency of feed utilization, have been studied. Kennedy and Moxley (1980) estimated the heritability of rhinitis incidence at 0.12 for three breeds of pigs. They also showed that single crosses and backcrosses showed only a small improvement over purebreds (1.1 and 3.4% respectively), whereas three-breed crosses showed a marked superiority over purebreds (22.1%). Crossbreeding was also found to improve rhinitis score by between 10.1 and 28.5% (Kennedy and Moxley 1980).

Future prospects

More movement of animals among countries and continents in future can be expected to ensure that the best available genetic material is combined to achieve breeding objectives. Advances in genetic engineering will have a great effect on the future of the swine industry. Advances in AI and related techniques should eventually make it possible to freeze semen and thus to increase the range of use of genetically superior boars. Advances in reproductive physiology should make estrus synchronization and superovulation easy procedures that breeders can perform on their premises. Reproductive problems such as infertility and extended weaning-to-conception intervals should be controlled.

Advances in piglet nutrition should allow artificial rearing of piglets on liquid or dried diet from only a few days after birth and should reduce the high postnatal mortality. New equipment to measure accurately body composition, ovulation rate, and other important traits should further aid in selection programs.

With rapid developments in computer technology, all farm operations could soon be controlled by computer, which would make breeding strategy and management decisions faster and more accurate.

EGG CHICKENS

R.W. Fairfull

In 1986, 23.5 million hens in Canada produced 491 million dozen eggs with a value of $512 million. Canadians consumed 17.6 dozen eggs per capita, down from a peak of about 25.0 dozen in 1957. The number of laying hens has remained relatively constant since about 1976, but has declined by about 19% from a peak of about 29.1 million hens in 1957.

The breeding industry for egg-production stocks of poultry is international, sophisticated, and highly competitive. Six or seven large breeding companies control most of the international market for commercial laying hens. However, countries such as Norway and Australia entirely exclude non-native breeding stock.

The egg market is divided into three segments, based on eggshell color: brown, tinted, or white. The basic stocks used to produce commercial layers in each of these categories differ. At least three primary strains or lines are usually used to produce hybrid, commercial laying stocks. The lines used may vary to fit different climates or markets. Genetic improvement of the commercial stock is based upon selection within pure lines or pure line selection based on cross performance. The major breeding companies devote considerable resources to maintaining or improving the genetic quality of their pure lines.

A commercial laying hen must have high performance in the complete array of essential traits: high egg production over a long laying period, large egg size, early sexual maturity, high fertility and hatchability, good viability, small body size, strong eggshells, superior interior egg quality, and good feed conversion. No commercial breeder expects to remain in business with a stock that is significantly poorer than that of the competitors in any of these essential sectors of performance.

Clayton (1968, 1972) was a proponent of the view that little if any genetic improvement had been achieved with layers. In the past, poor records, major improvements in environments and disease control, and poor design of commercial stock comparisons have made it virtually impossible to separate genetic improvement from other factors affecting performance. However, despite these complications most of his colleagues disagreed with this view (Dickerson and Mather 1976, Foster and Weatherup 1977, Flock 1978, 1979) as did Clayton (1978) himself.

Flock (1978, 1979) pointed out that the number of eggs per hen housed has at least doubled in the past 20 to 30 years in conjunction with a fivefold increase in the number of eggs that can be purchased for an hour's labor. On the basis of results from random sample tests, Dickerson and Mather (1976) and Foster and Weatherup (1977) concluded that genetic improvement has taken place both in average and in individual stocks. This last point is important because part of the improvement over years has resulted from the elimination of breeding companies.

The estimates of time trends in commercial stocks are based on two types of random sample tests: the United States Department of Agriculture (USDA) 2-year combined summaries of random sample egg production tests (Table 9) and the central Canada egg production tests (Table 10). The significance of random sample testing has been discussed extensively by Dickerson (1965) and Fox (1978). None of the tests summarized in the USDA compendium of North American random sample tests had control strains, so the trends estimated from that source are not exclusively genetic ones. The trends estimated from the central Canada egg production tests are based on deviations from a control strain and therefore represent genetic trends. Trends were estimated by regressing the means (or mean deviations) for each character over years. In both cases, the same two widely used commercial stocks (B and C), present in all years, are included separately.

The years between 1970 and 1980 are particularly good ones from which to estimate genetic progress because during that time there were no major improvements of environmental factors (Flock 1979). Marek's disease vaccination was widely introduced in 1970 and new information regarding lymphoid leukosis virus (LLV) infection had no effect until after 1980 (Gavora et al. 1980).

Yield traits

Egg production, the major yield trait, is a function of sexual maturity, rate of egg production, and viability. The genetic potential for egg production in commercial stocks has increased substantially (see Tables 9 and 10). The lowest estimate of increased genetic potential indicates an increase of 13 eggs per hen over the decade for commercial stock B, which had extremely high egg production potential to start (see Table 10). Concurrently, the genetic potential for egg size increased as estimated from egg weight and percentage extra-large plus large eggs (see Table 10). In a long-term multiple-trait selection study, it was shown that sustained gains per generation of one to two eggs and 0.3-g egg weight can be achieved even with relatively small populations (Gowe and Fairfull 1984, 1985).

An environmental factor may have contributed to a reduction in egg size, as the trend until 1977 was downward (see Table 9). Compared with egg production, genetic improvement for egg size was small. This result was to be expected because producers are aiming at an optimum egg size rather than continual improvement. More recently commercial breeders with stocks that lay large eggs have reduced the egg size potential of their stocks in response to market pressures.

The trend for net income to increase (see Tables 9 and 10) is difficult to understand. Net income is affected by a complex interaction of costs and returns. However, throughout the 1970s costs increased substantially relative to returns (Adolph 1976, Bonzer and Plumart 1976, Plumart and Bonzer 1976). This trend indicates that egg-producing stocks of poultry have maintained their profitability through genetic improvement.

Table 9 Average annual phenotypic change in performance of commercial egg layers estimated from a combined mean of all North American random sample tests, 1970–1977

Traits	Commercial stock		
	All	B	C
Yield			
Egg production (no.)	4.0	5.6	2.0
Egg weight (g)	−0.23	−0.05	−0.20
Extra-large & large eggs (%)	−2.1	−0.6	−1.5
Net income ($)	0.65	0.65	0.48
Product quality			
Shell quality (egg specific gravity)	0.05	−0.06	0.02
Haugh units	−0.38	−0.05	−0.32
Blood spots (%)	0.02	−0.01	−0.01
Meat spots (%)	−0.06	0.01	0.01
Cost reducing			
Sexual maturity (days)	−2.5	−2.4	−1.0
Feed conversion	−0.019	−0.036	−0.004
Body weight (g)	−51.0	−32.0	−29.0
Viability (%)	0.18	0.03	0.14
Laying viability (%)	0.83	0.83	0.81

Product quality

The genetic potential in the egg quality traits has not changed substantially (see Tables 9 and 10). The most significant change has been a minor increase in eggshell quality (strength). This stability indicates that the high interior and exterior quality of eggs has been maintained whereas egg yield has increased substantially. Experimental results support this contention. Studies by Rhoda et al. (1977), Friars et al. (1978), and Akbar et al. (1983) showed that neither yolk nor albumen has shown dilution as a result of selection and that albumen percentage solids may have increased slightly; however, the yolk-to-albumen ratio has shifted in favor of albumen (i.e., the amount of albumen has increased more than the amount of yolk). Experimental populations have shown that substantial improvements in egg quality traits are possible (Gowe and Fairfull 1980).

Table 10 Average annual genetic change in performance of commercial egg layers estimated from central Canada egg production tests, 1970–1980

	Commercial stock		
Traits	All	B	C
Yield			
Egg production (no.)	3.2	1.3	2.1
Egg weight (g)	0.19	0.28	0.09
Extra-large & large eggs (%)	1.3	1.5	0.9
Net income ($)	0.29	0.28	0.29
Product quality			
Shell quality (egg specific gravity)	0.018	0.004	0.130
Haugh units	−0.06	−0.16	0.07
Blood spots (%)	0.02	0.02	−0.06
Meat spots (%)	0.02	−0.01	−0.01
Cost reducing			
Sexual maturity (days)	−0.9	−1.6	−0.4
Feed conversion	−0.033	−0.033	−0.026
Body weight (g)	−0.1	−0.2	−0.2
Viability (%)	0.15	−0.73	0.51
Laying viability (%)	0.36	−0.39	0.60

Cost reduction

Commercial stocks have the genetic potential to lay eggs at increasingly earlier ages (see Tables 9 and 10). The earlier onset of sexual maturity has contributed to an increase in yield potential and to a decrease in costs by increasing the number of days on which eggs can be laid and by reducing the length of time hens need be maintained without returns. The genetic potential of commercial stocks for efficiently converting feed to high-quality protein has increased enormously, which has been an indirect benefit of increased egg production and size. However, genetic variation for feed conversion is independent of egg mass and body size, so that direct selection could possibly increase the rate of response (Fairfull and Gowe 1979).

Changes in the genetic potential for body size were very minor (see Tables 9 and 10). Reduction of body size is desirable in laying hens as smaller size reduces the energy requirements for maintenance. However, in laying hens smaller body size is usually genetically associated with smaller egg size and lower numbers of eggs. Therefore, to maintain a low body weight and at the same time to increase egg numbers and egg weight is an accomplishment.

The genetic potential for viability has increased in commercial stocks (see Tables 9 and 10). Improved viability profoundly increases egg yield and reduces cost of egg production. Breeders are now using genes at the histocompatibility complex that confer genetic resistance to Marek's disease (Gavora and Spencer 1979). Several haplotypes that increase genetic resistance to Marek's disease have been identified (Longnecker et al. 1976, Briles et al. 1977, Gavora et al. 1982*a*). Even when birds are vaccinated, viability is higher if they are genetically resistant to Marek's disease (Spencer et al. 1974).

Avian lymphoid leukosis reduces the efficacy of genetic selection (Gavora et al. 1980). Relaxation of selection during production of commercial hybrids contributes to substantially reduced performance through an increased incidence of infected birds. Infected birds usually produce less and are mostly eliminated from reproduction in selected lines. At present, many commercial breeders are eradicating this virus from their flocks.

Future prospects

Egg-laying stocks of poultry have a substantially improved genetic potential over those of a decade ago. This genetic improvement has been realized mainly in the yield and cost reducing traits. Egg-quality traits have essentially been maintained at high levels, with only minor improvements.

Three factors have influenced the improvement in poultry egg stocks: multiple-trait selection; crossing strains or breeds; and the elimination of poorer lines, strains, or commercial stocks. Multiple-trait selection has been the most important factor in the continued improvement of poultry egg stocks. The gains made by each generation are cumulative as long as selection is practiced. Sophisticated methods are used to identify high-performance birds. They must have high performance for all traits of economic importance: high egg production, a long laying period, large egg size, early sexual maturity, high fertility and hatchability, excellent viability, small body size, strong eggshells, and superior egg quality.

Crossing strains or breeds to take advantage of heterosis and other effects follows in importance. Heterosis adds more than 8% to egg production and 6% to efficiency. Crossing also allows the breeder to combine the strong points of different lines or to compensate for a weakness in an otherwise superior line.

Finally, poor genotypes have been ruthlessly eliminated. The most common method has been through the closure of breeding companies, thousands of which have gone out of business since the turn of the century. However, the lines contributing to commercial stocks are changed also. Lines are developed and tested constantly, and the lines contributing to a particular commercial stock are replaced as necessary.

In the future, multiple-trait selection and crossing will continue to be important. Breeders will increase the frequency of genes that confer resistance to important diseases. Where possible, diseases will be eradicated from primary breeder flocks. Freedom from disease will not only result in improved performance but will also improve the accuracy of selection and thereby increase genetic progress.

Egg production will remain a trait of primary importance. Traits for cost reduction, especially feed conversion, will increase in importance. The remaining traits will continue to be important, but their relative importance will probably not change.

Sophisticated biological techniques, such as gene transfer, will be applied to egg-laying stocks of chickens. At first, these techniques will be limited to genes or regions of chromosomes with identified major effects.

MEAT CHICKENS

J.R. Chambers

Industrially, the production of meat chickens in Canada exceeded $1 billion in 1982 and continues to increase. Canadian production accounted for roughly 93% of domestic consumption of over 425 million kg of eviscerated chickens. Per capita consumption exceeded 17 kg.

Yield traits

Breeders have markedly increased the growth rate of broilers during the past three decades. Commercial broilers available in 1978 were shown to grow at least twice as fast as broilers from control lines. The control lines used in these comparisons were established by 1958 from breeding stocks obtained in 1955 and have since been maintained without artificial selection (Marks 1979, Chambers et al. 1981). Selection for increased body weight is associated with positive gains in appetite and feed conversion (Siegel and Wisman 1966, Wilson 1969). When restricted to the same daily feed intake as broilers from slow-growing lines, broilers from rapidly gaining lines grew little faster and only slightly more efficiently (Proudman et al. 1970).

Product quality

Carcass fleshing, conformation, and finish reflect aesthetic aspects of carcass quality. Quantitative tests to measure progress in this area could not be found; however, the general excellence observed for these traits indicates that adequate breeding progress is being achieved. Greater numbers of excessively fat broilers have led to consumer and processor complaints during the past decade. Excess fatness results from increases in both carcass fat and abdominal fat. These two traits are correlated highly positively (Griffiths et al. 1978, Becker et al. 1979). More than 2% of the weight of fat broilers may consist of gizzard fat, a component of abdominal fat, which is discarded during evisceration. The dressing percentage, that proportion of the live broiler weight consisting of the eviscerated carcass, is thus reduced in fat broilers. In addition, leaf fat (abdominal fat left in the eviscerated carcass) may exceed 3% of the weight of fat broilers. This fat is frequently removed and discarded by the consumer before the product is cooked. Abdominal fatness may be reduced by selection (Leclercq et al. 1980) or as a correlated response to selection for improved feed conversion (Pym and Solvyns 1979). Only recently have these procedures been applied in the commercial breeding of poultry for meat.

Among the major chemical components of the carcass, the amounts of protein, moisture, and ash are highly correlated; however, the fat content of the carcass is more independent. Because of the interrelationships among these components when they are expressed as proportions of the total carcass, an increased fat content dilutes the proportions of the other components.

Increased fatness is associated with less efficient feed conversion, both phenotypically (Washburn et al. 1975) and genetically (Pym and Solvyns 1979, Leclercq et al. 1980). Negative heterosis for measures of adiposity was observed among crosses of Japanese quail (Wyatt et al. 1982). This relationship may account for the superior feed efficiency of strain crosses versus pure strains of broilers.

Proportions of the various carcass cuts have not changed. Differences between modern broilers and those of the fifties are few and small, despite vast differences in growth rate (Chambers et al. 1981). The modest differences observed probably represent developmental changes. As age progresses, the proportion of neck, wings, and breast in the carcass increases whereas that of the drumsticks, and back decreases at a declining rate to 10 weeks of age (Leeson and Summers 1980).

Cost reduction

Feed costs frequently exceed 60% of the production costs of broilers. However, breeders have been reluctant to measure feed efficiency, or its inverse, feed conversion, because special facilities and more labor are required to measure individual feed consumption.

Comparison of the feed conversion of modern broilers to a constant age (1978) with that of broilers maintained unchanged since 1958 shows that modern broilers are only slightly superior, 2.0 vs. 2.1

(Marks 1979) and 1.9 vs. 2.0 (Chambers et al. 1981). More meaningful results have been obtained from comparisons based on tests to similar weight. The slower-growing strains of broilers included in the studies by Marks and by Chambers et al. would have required more time to attain the required weight and their feed conversion would have increased markedly.

Broiler production costs have been minimized by attempts to improve production of broiler chicks. Few of the component traits of high broiler performance are favorably related to both chick numbers and broiler performance and only modest progress is evident. Hence, number of eggs per hen, percentage of fertile eggs, and hatchability of fertile eggs set are generally poorer for broiler parent than for Leghorn stocks. Another characteristic of broiler dam stocks is the relatively high percentage of defective eggs that is associated with irregular oviposition (Jaap and Muir 1968, Reddy and Siegel 1976). This phenomenon gives rise to double-yolked eggs and to single-yolked eggs with either thin, chalky, or dented shells. These eggs are unsuitable for hatching.

Much potential for improvement exists in cost reduction. Decreased mortality and reduced incidence of crippling and of disease in broiler and in parent flocks increases production of broilers and reduces the cost of broiler chicks. Increases in the incidence of acute death syndrome (or heart failure) and of crippling in broilers, two conditions associated with increased growth rate, are contributing to major economic losses in broiler production. Acute death syndrome routinely accounts for a major proportion of broiler mortality (Brigden and Riddell 1975). Economic losses resulting from disease arise not only from mortality but also from reduced performance caused by subclinical infections. Progeny of broiler dams infected with lymphoid leukosis virus have lower body weights (Gavora et al. 1982*b*). With one exception involving Marek's disease (Friars et al. 1972) there is little evidence of selection for disease resistance in commercial broiler lines.

Past progress

The genetic improvement of the growth rate of broilers has been favored by broiler breeders because a live chicken is easily measured with minimal disturbance to the flock. Moreover, body weight between 6 and 12 weeks of age is moderately to highly heritable (Kinney 1969). Siegel (1962) reported a median value of 0.41 in a review involving 176 heritabilities. The proportion of improvement in growth rate that results from the adoption of superior lines for the crossbreeding system as opposed to the proportion produced by the selection of superior individuals within lines is unknown. It is known, however, that intense selection for either broiler weight or weight gain during a phase of broiler growth was adopted by commercial breeders during the 1970s and continues to be practiced.

Increases in growth rate have been accompanied by increased appetite and improved feed conversion (Siegel and Wisman 1966, Wilson 1969, Pym and Nicholls 1979). Rapid growth is not possible if feed intake is restricted (Proudman et al. 1970).

Carcass fleshing and conformation are gauged by various anatomical measurements, such as breast angle, keel length, chest width, and body depth. Differences in these traits are moderately to highly heritable (Merritt 1966, Ricard and Rouvier 1968), which makes rapid genetic improvement of these traits possible.

The problem of excess fatness in broilers could have been averted by using suitable breeding programs. Fatness is not only a variable trait, exhibiting coefficients of variation that frequently exceed 25% (Ricard and Rouvier 1969, Becker et al. 1979, Chambers et al. 1981), but it is also a highly heritable one (Ricard and Rouvier 1967, 1969; Leclercq et al. 1980, Chambers and Gavora 1982, Chambers et al. 1984). Differences in abdominal fatness among strains have been reported (Edwards and Denman 1975, Farr et al. 1977, van Middelkoop et al. 1977, and Griffiths et al. 1978). Progress in genetically reducing broiler fatness has been delayed by difficulties encountered in obtaining accurate measurements. A direct measurement of fatness can only be taken after the chicken is slaughtered. Genetic improvement can be made through selection of sibs. Fatness cannot be predicted accurately from measurements on a live broiler. Moreover, only within the past decade have breeders become aware of the seriousness of the problem and appreciated its negative influence on feed conversion (Washburn et al. 1975, Pym and Solvyns 1979, Leclercq et al. 1980, Chambers and Gavora 1982, Chambers et al. 1984).

Measuring the feed efficiency of individual chickens is costly, not only in terms of labor but also in terms of facilities. Therefore, indirect improvement of feed efficiency, as a correlated response to selection for rapid weight gain, was recommended by Fox and Bohren (1954) and Wilson (1969). Breeders have followed this recommendation until recently. Feed efficiency is now, however, being measured directly because a major proportion of the variation in efficiency was shown to exist independent of weight gain (Guill and Washburn 1974, Pym and Nicholls 1979, Chambers et al. 1983). Strong, favorable correlations between carcass leanness and feed conversion were also found.

The components of reproductive efficiency are only lowly to moderately heritable (Kinney 1969, Fiser and Chambers 1981), and they are antagonistically related not only to broiler growth rate (Soller et al. 1965) but also frequently among themselves. The limited progress that has been made results from genetic selection for appropriate traits within lines and from selection of superior specialized lines for the production of sires and dams. The improvement of production efficiency through selecting specialized dam lines would be little better than that achieved through selection within lines for meat productivity. However, the margin for success is much greater through the selection of specialized dam lines because negative relationships exist between productivity and female reproductive performance (Moav and Hill 1966).

Problems such as acute death syndrome and crippling in broilers have increased in frequency as the growth rate has been increased. This relationship suggests the development of a physiological imbalance. Specific causes of acute death syndrome are unknown; however, differences in incidence exist among broiler strains (Brigden and Riddell 1975). Furthermore, the incidence of tibial dyschondroplasia, a common type of crippling in broilers, can also be changed by selection (Riddell 1976, Sheridan et al. 1978). These findings suggest that these conditions could have been reduced if they had been considered in breeding programs.

The prevention of diseases either by vaccination or by the maintenance of germ-free flocks and environments has been preferred to prevention through genetic selection for resistance to diseases. These programs, if successful, permit the selection pressure that would have been used for disease resistance, to be used to improve other economic traits.

Future prospects

In the future, increased, multiple-trait specialized selection will be applied within sire or dam lines used for production of crossbred broilers. Improvement in growth rate will continue at a slower pace because of multiple-trait selection, greater emphasis on antagonistically related reproduction traits, and attempts to reduce the physiological imbalance. Rapid genetic reduction of broiler fatness can be expected; however, gains will be costly unless traits are found that can be measured in live birds to predict effectively carcass or abdominal fatness. Feed efficiency will improve through direct selection capitalizing either on variation independent of growth rate or on a correlated response to reduced broiler fatness. Multiple-trait selection should improve reproductive efficiency; however, a major advance will be achieved if the dwarf broiler dam (Japp and Mohammadian 1969, Guillaume 1976) is widely adopted to produce competitive broiler progeny. The dwarf mother consumes 25% less feed, requires less housing space, produces fewer defective eggs, and produces slightly lighter progeny because of smaller hatching egg size and the dwarf gene carried by males. To minimize broiler production costs, genetic selection and management changes to reduce acute death syndrome and crippling will be necessary.

GENERAL PROGRESS AND PROSPECTS

J.S. Gavora

Although the situation in the various species and commodities already discussed varies considerably, examination of animal improvement over the past two decades and beyond demonstrates that changes in emphasis have occurred on selection of traits for yield, product quality, and cost reduction.

Historically, emphasis was placed on the improvement of overall yield of the commodity per animal, through increased product volume or production rate (growth). More recently, increasing emphasis was placed on improving product quality, as a reflection of increased sophistication of the market and product-grading systems. Traits for cost reduction such as early sexual maturity, viability, and disease resistance, as well as feed efficiency, have only recently become the subject of breeders' attention. In the past decade, more emphasis has been placed on establishing a balance in these traits, although market conditions often still dictate selection for one particular trait.

The review of progress achieved to date also demonstrates that animal breeders were able to change genetically any trait identified as important. Even traits with low heritability, which commonly have observable genetic variation but an even larger environmental variation, were amenable to significant improvements when suitable genetic techniques were applied.

Both additive and nonadditive genetic variation continued to be used successfully in animal improvement. The relative emphasis on selection, which uses additive genetic variation, and on crossbreeding, which takes advantage of nonadditive genetic variation, varied among individual species. The use of crossbreeding was most limited in dairy cattle. A breed of cattle has yet to be found that produces progeny with competitive milk production performance under temperate conditions when it is crossed with the Holstein.

All selection efforts, including extremely intensive selection in chickens for meat, failed to demonstrate the emergence of selection limits in animal breeding. This finding is encouraging for the future and agrees with conclusions reached by Kennedy (1984), Fredeen (1984), and Hunton (1984), who discussed selection limits in dairy cattle, swine, and poultry, respectively. Intuitively, we generally assume the existence of such limits, because plateaus were experimentally demonstrated in single-trait selection experiments. Nevertheless, selection limits do not seem to hamper progress in animal breeding, particularly where multiple-trait selection is applied to populations of adequate size.

Although limits did not restrict progress in selection, intensive selection for rapid growth and carcass conformation did result in an increase in the frequency of developmental disorders, for example, increasingly serious problems in the skeletal muscle and legs.

Contributing factors

The overall improvement in farm animals and poultry continues to result mainly from selection. The use of inbreeding has been very limited. Crossbreeding has been applied among breeds, often accompanied by breed substitution, as well as within breeds among strains or lines. Expansion of the use of computers and rapid increases in computer power have allowed more efficient handling of large amounts of data from animal and poultry breeding, as well as the testing of theoretical expectations in computer simulation studies. Use of synthetic genetic bases, primarily in poultry breeding, is leading to the abandonment of the concept of breeds in favor of strains or lines within a production type.

Improvements in the reproductive efficiency of species with a slow reproductive rate have begun to exert an influence on female reproduction but their effects are not yet widespread. Increased rates of male reproduction through the use of artificial insemination continue to have a major influence on genetic progress since work in this area began some 30 to 40 years ago.

The use of major genes as markers or components of quantitative traits has had a limited effect in some species but shows promise for the future especially through use of DNA polymorphisms as markers.

Future prospects

In conventional selection, a more balanced approach to multiple-trait selection can be anticipated. Multilevel information on multiple traits of families and individuals will be used more frequently, as practically unlimited computing capacity becomes readily available. Marker traits will be used more widely, especially for traits difficult or impossible to measure directly. Reproductive manipulation, molecular and biochemical genetics, and genetic engineering are providing new approaches that will be gradually integrated into livestock improvement programs. Selection emphasis in future will be placed on the various traits that better reflect the physiological importance to the species, as well as economic importance to the producer. Traits for product quality and cost reduction will probably receive increased emphasis in selection as progress in yield traits gradually slows.

Increasing consumer awareness is adding a new dimension to animal production, and public resistance to the use of feed additives and chemicals, and even to vaccination and medication will pose new challenges to animal breeders.

Animal welfare, not dealt with above, is an issue that will continue to be of concern. Both genetic and environmental changes will be used to solve animal welfare problems, particularly as more rational positions are taken by special interest groups (Beilharz 1982).

CONTRIBUTIONS OF SCIENTIFIC RESEARCH TO ANIMAL BREEDING

J.S. Gavora

The various areas of animal research that are discussed in this section were selected more-or-less arbitrarily to represent a mixture of well-defined scientific disciplines and not-so-well-defined areas of research. A consideration of their past and future contributions to animal breeding should present a picture of the state of the art in each field. The discussion of quantitative and statistical genetics was given a prominent position because it forms the backbone of modern animal breeding. An examination of the role of biochemical and physiological genetics follows. Although its contribution to progress achieved in animal breeding was limited, the future usefulness of this discipline in elucidating the structure and function of genes and genomes and in directly contributing to animal improvement can hardly be overestimated. A separate review is devoted to disease resistance genetics because this subject, which requires immunological and pathological expertise, could not easily be accommodated under any other heading.

Inclusion of the discussion on the genetic effects of advances in reproductive physiology was justified not only because of its past contribution to animal breeding, but mainly because of the future role this area of research is anticipated to play. Its influence is expected to affect profoundly the genetic progress from animal breeding and potentially also the entire structure of the breeding industry. The final part of the review deals with molecular genetics. This discipline has practically no past with regard to animal breeding, but its future is enormous, one that is difficult to grasp and assess.

Discussions of all topics deal with past and future effects of each area. An attempt is made to summarize and assess the interactions among the various disciplines and areas of animal breeding research.

QUANTITATIVE AND STATISTICAL GENETICS

A.J. Lee

Animal breeding is a systems science that incorporates genetics, reproductive physiology, statistics, computer science, and animal husbandry in a highly interactive fashion to maximize genetic improvement. The basic concepts of selection and specific mating for genetic improvement date back to early domestication and were first formally expressed by Darwin (1860). Progeny testing, mild inbreeding, performance recording, and statistical approaches without formal genetic input (Galton 1897; Pearson 1897, 1902;

Pearson and Lee 1903) predate the rediscovery of Mendel's work. Applied animal breeding without a formal genetic foundation was thus established well before the 20th century.

The foundations of quantitative genetics based on mendelian inheritance and a formal basis for measuring inbreeding and relationship were provided by Fisher (1918) and Wright (1921). The statistical analysis theme was strengthened by the ideas of Fisher (1925) and Yates (1934). Lush (1937) of Iowa and his students worked in the use of simple quantitative genetics, statistics, and knowledge of animal husbandry to develop programs for genetic improvement through performance recording, adjustment of data for systematic nongenetic factors, evaluation, and selection.

Recent history

Quantitative genetics Malécot's 1948 concept of identity by descent of individual and multiple genes at the same or different loci permitted epistatic relationships between individuals to be partitioned into component parts. This work was followed in 1954 by the partitioning of epistatic genetic effects in the genetic variance (Cockerham 1954, Anderson and Kempthorne 1954, Kempthorne 1954). The books by Kempthorne (1957) and Falconer (1960) are good summaries of knowledge at that time. This approach was extended to the genetic covariance between traits by Mode and Robinson (1959) and to inbred relatives by Harris (1964).

Subsequently, Willham (1963, 1972) provided a theoretical basis for considering inherited maternal effects and thus extended the original work of Dickerson (1947). This partitioning of genetic variation and covariation provided the basis of a better understanding of heterosis or hybrid vigor in crossbreds and the lack of similar performance in reciprocal crosses. However, little consideration has been given to quantitative genetic theory for nonmendelian inheritance, such as could occur with replicating DNA or RNA that is cytoplasmically transmitted.

As Hazel and Lamoreaux (1947) and Comstock and Robinson (1948) were estimating the magnitude of "nicking" effects while eliminating environmental and genotype by environment interactions, Crow (1948) examined the theoretical basis of hybrid vigor from the viewpoint of dominance and overdominance. Almost simultaneously Comstock et al. (1949) proposed reciprocal recurrent selection as a means of using both general and specific combining ability for genetic improvement. The book *Heterosis*, edited by Gowen (1952), brings together much of the work at theoretical and applied levels concerning estimation and use of hybrid vigor, heterosis, or specific combining ability in both plants and animals. Henderson's report in that book appears to have been the first consideration of lines as being random rather than fixed effects in the statistical model. Bradford et al. (1958) provided a thorough consideration of later results in swine. Analyses of diallel crosses have also been considered by Mather (1949), Hayman (1954, 1958, 1960), and Griffing (1956). Lerner (1950, 1954, 1958) provided a broad view of selection, animal improvement, and the role of an integrated, biologically interactive organism in evolution.

Statistical methodology Advances in statistical theory and methods have had a major effect on animal breeding. Hazel (1946) extended Yates' analysis of unbalanced data to the analysis of covariance. Shortly after Crump (1951) provided a concise statement of the status of variance component analysis, Henderson (1953) proposed three methods of estimating variance and covariance components. Use of these methods to estimate sire variance or covariance, and hence heritability or genetic correlation, provided the estimates of parameters required in constructing selection indexes.

Subsequently, best quadratic unbiased (BQUE), restricted maximum likelihood (REML), and maximum likelihood (ML) methods were developed by authors such as Searle, Henderson, Corbeil, Thompson, C.R. Rao, J.N.K. Rao, Harley, and Hemmerle. They are thoroughly and concisely reviewed by Harville (1977) with an excellent explanation of the relationship between different formulations and procedures for the two-way mixed model (Harville 1978). Specific consideration of methods for estimating the variance components when culling exists has been given by Curnow (1961) and Thompson (1973). Methods for estimating maternal effects using records on parents and offspring were similarly treated by Hill and Nicholas (1974) and Thompson (1976). Schaeffer et al. (1978) and Schaeffer (1981), among others, have further refined BQUE, REML, and ML methods for particular application in recent years. The major unsolved problem is to find algebraic simplifications that will make computation feasible for the large, unbalanced, multivariate sets of data encountered in animal breeding.

Selection Smith (1936) first applied Fisher's linear discriminant approach to plant selection. Hazel and Lush (1942) then demonstrated that linear discriminant methods or selection index methods were superior to tandem selection or selection using independent culling levels for genetically improving a known linear combination of traits. Hazel (1943) provided a genetic basis for selection indexes, which had previously been considered primarily a statistical tool. Lush (1947) used the selection index approach to evaluate the relative importance of an individual's performance in selection, as well as to evaluate the importance of performance of relatives. A formal statistical basis for selection indexes was provided by Cochran (1951). Henderson and co-workers (1959) showed that selection indexes, adjusted for systematic environmental effects, could be obtained by solving the normal equations of least squares after a simple modification. These modified least squares equations are now known to form a convenient computational basis for the estimation of the variance and covariance components using the BQUE, REML, and ML methods already mentioned. Henderson (1963) demonstrated that selection indexes are appropriate, at least for ranking, when unequal amounts of information are available on the individuals being evaluated.

Kempthorne and Nordskog (1959) first considered selection indexes designed to improve a linear combination of traits while forcing expected genetic change to zero for one or more traits. Harville (1974) provided a comprehensive picture of selection methods that impose constraints on the desired responses in one or more traits. Van Vleck (1970, 1976) provided selection index methods for considering maternal and grandmaternal genetic and environmental effects. A thorough consideration of selection index methods when data are subject to culling was provided by Henderson (1975*a*) and Thompson (1979). Most of the methods up to that time dealt with either multiple traits without a classification model or with single traits in complex designs.

Complex design models dealing with multiple traits were identified by Henderson (1973) and were examined in greater detail by Henderson and Quaas (1976). Lee (1979) derived a simplification of multiple-trait selection indexes under complex models, which is applicable when all traits are recorded on each individual and when the same classification model applies to each trait. Hayes and Hill (1980) proposed a canonical transformation of variables for multiple-trait evaluation in simple models. This development was followed by independent, simultaneous derivation of the extension to complex models by Foulley et al. (1982) and Lee (1983). Multiple-trait evaluation under complex models has been used in beef cattle on a fairly wide scale, led by the work of Schaeffer and Wilton (1975) and Schaeffer et al. (1980).

Use of appropriate functions of traits or economic weightings of traits has received moderate attention, for example in beef cattle. Management and genetic factors were considered in economic models, using linear programming by Cartwright et al. (1975) and Wilton and Morris (1976). Use of multiple-trait evaluations of animals in linear programming models for assessing economic returns was considered by Wilton (1982).

Before 1975, inclusion of the relationship between sires or individuals in selection indexes was impractical because the inverse of the relationship matrix was required. Henderson (1975*b*, 1976) derived a rapid and easy method of computing the inverse relationship matrix, based on the triangular or Cholesky decomposition of a symmetric matrix. This major breakthrough permits use of relationships in selection indexes and in estimation of variance and covariance components for large populations. Before this advance, all sires being evaluated were considered unrelated even though some were sons, grandsons, or half brothers of each other. The major current problem is deriving practical, algebraic simplifications and computing methods to permit multiple-trait, mixed-model selection indexes when all traits are not recorded on each individual, possibly because of selection and culling.

None of the statistical methods derived in the past 20 years would be of any practical value in animal breeding without the major improvements in capacity, speed, and economy of electronic computers. Hundreds or thousands of equations in a like number of unknowns must be solved simultaneously to obtain national or regional evaluations of sires and cows for beef and dairy cattle. Hence, statistical and computing developments have been major factors in effectively using quantitative genetics for animal improvement.

Mating designs Methods for estimating genetic parameters and for creating and measuring genetic improvement have also seen major improvement. Dickerson and Hazel (1944) examined progeny testing whereas Dempster and Lerner (1947) examined breeding plans in poultry using full- and half-sib information. Polge et al. (1949) discovered the possibility of freezing bovine semen, a development that permitted testing of cattle progeny on a much wider scale than was previously possible. The optimum balance between number of bulls to include in a progeny test, the number of progeny tested per bull, and intensity of subsequent selection has been examined in detail (Robertson and Rendel 1950, Robertson 1957, Rendel 1959, van Vleck 1964). Skjervold (1963) and Skjervold and Langholz (1964) considered similar plans for smaller populations. They concluded that extensive use of young, pedigree-selected bulls sired primarily by progeny-tested bulls would increase the rate of genetic improvement more dramatically than the alternatives suggested by van Vleck (1964) for very large populations. The effects of timing and interest rates on the economic return received from breeding programs were first considered by Hill (1971*a*). Hudson et al. (1980) examined various designs for testing the weaning weight and the calving ease of progeny in beef cattle. With the advent of ova transplant technology, fertilized eggs from highly selected parents can be used widely. Nicholas and Smith (1983) indicated some of the possibilities for improved rates of genetic gain using these methods.

Breeding experiments were designed by Robertson (1959) to obtain optimum numbers of progeny for estimating genetic correlations. These designs were later generalized by Hill (1971*b*). Hill and Thompson (1977) considered designs in which data from both parent and offspring are used for the selection of parents. This work represents the link between experimental design, quantitative genetics, and data analysis.

A clear definition of the theoretical basis of random-bred control strains and practical use of this theory with particular reference to poultry was provided by Gowe et al. (1959). This design permits the accurate measurement of environmental trends on any number of traits over long periods without having to retain parents for more than one generation. The genetic change in selected lines maintained under the same environment can then be measured as a deviation from controls. This design has been used extensively in poultry breeding and in laboratory species and has also had a few applications in larger animals. Hill (1972*a*,*b*) thoroughly considered the usefulness of estimating realized heritabilities and genetic correlations from one-way or divergent selection experiments. Goodwin et al. (1959) examined the use of repeat mating, i.e., holding parents over for use in two or more generations. Differences in performance between progeny of the same parents in adjacent years provide a measure of environmental change and hence a basis for evaluating genetic change. Hickman and Freeman (1968) expanded on this approach to develop a practical method for creating and measuring genetic trend in populations having overlapping generations, with particular reference to dairy cattle. These improvements in mating and selection designs have made a major contribution to the increase in the rate of genetic improvement and its accurate measurement.

Present status

Animal breeding finds itself today in about the same state as a partially completed jig-saw puzzle. The outside frame and a large part of one corner have been completed and several other groups of pieces have been assembled but no one has yet been able to tie it all together. With few exceptions, selection for one trait or a few traits has been highly successful, assuming essentially additive genetic inheritance, and this success is generally typical of animal breeding practice. Estimates of heritabilities for a variety of important or potentially important traits and their genetic correlations are numerous in all species.

Few reports if any, however, have been able to present a comprehensive, multivariate consideration of important traits. Crossbreeding has been used, primarily in meat-animal species and poultry, to take advantage of heterosis and major additive genetic differences between breeds or strains. Few studies have examined the joint use of selection and crossbreeding to maximize genetic potential for productivity. A noteworthy exception is the Canadian national cooperative dairy cattle breeding project (McAllister et al. 1978). A few major genes affecting economically important traits have been discovered, such as those controlling dwarfism in beef cattle and poultry, double muscling in beef cattle, and the porcine stress syndrome in pigs. Several genetic defects, such as syndactylism and osteoporosis, have been examined in detail, particularly by Huston and Leipold in Kansas (Leipold 1986). However, each is usually dealt with as a single locus problem to be eliminated while proceeding with selection.

Ova transplant and storage technology and other new developments in reproduction, which are discussed later, are developing rapidly and may soon be economical on a large scale. They open up many new opportunities in animal breeding research, particularly in species with low reproductive rates. We still have little knowledge of the biological basis for genetic differences in primary production traits, such as growth, milk yield, or rate of egg production. Despite significant advances in animal breeding in recent years, major areas of our knowledge remain seriously limited.

The future

During the next 25 years, animal breeding should make advances in several areas. Many questions requiring study, such as the biological basis of major differences in quantitative traits, will only be answered through well-designed genetic experiments on farm animals rather than extensive statistical analysis of field data. Improved statistical methodology and computer technology will continue to play a major role in effectively analyzing data and in performing genetic evaluations of large populations in industry. However, emphasis will shift toward comprehensive, multivariate analysis, away from the univariate or bivariate analyses done at present. The capability for economically collecting and storing large numbers of fertilized ova from specific matings in species with low reproductive rates will be improved. Genetic research with cattle to examine maternal and nonadditive genetic effects will thus become more practical to conduct.

Research on animal breeding methods will emphasize the use of all of these developments to determine selection and mating schemes that fully use additive and nonadditive genetic variance in breeding for overall productive efficiency considering all economically important traits. Attainment of this goal will require a greater appreciation of the economic evaluation of farm animal production systems. Many of these approaches are included in the national cooperative dairy cattle breeding project of Agriculture Canada (McAllister et al. 1978). In general, this comprehensive approach to animal breeding will include a much larger quantitative genetic input than has been the case in the past.

Sophisticated statistical analysis, economic modeling, and detailed knowledge of interactions of genotypes with management programs (systems analysis) will become essential. The new opportunities created by rapidly evolving reproductive techniques will have to be fully evaluated in context. The complex interaction of genetics, statistics, computing, husbandry, and reproduction techniques will be accentuated in developing optimum, applied breeding programs.

A major goal could be the discovery of the biological basis for genetic differences between strains and sire groups for primary production traits. Although we know the basic biochemical pathways by which feed is digested, absorbed, and converted into muscle, milk, wool, or eggs, we know almost nothing about the mechanisms that control the rate and limits of conversion and thereby that determine differences in productivity. To attack this problem effectively, research teams must be established to study the genetic control of biochemical and physiological systems that are highly variable both between animals within a species and over time within an animal. These control systems are likely to be complex and highly interactive, just as the basic metabolic pathways are. Hence, expertise in sophisticated statistical methodology available in quantitative genetics, in combination with biochemical and molecular genetic techniques, may be vitally important in determining the exact nature of the control system. With some basic understanding of these biological systems, genetic engineering techniques may be, in time, successfully applied to improving the genetic potential for performance in farm animals.

One interesting paradox in animal breeding is that much of the genetic variation observed for quantitative production traits is additive even though nearly all the relevant biochemical pathways of metabolism and their endocrinological control are highly interactive. Research is needed urgently to elucidate this seeming contradiction. The collaboration of quantitative geneticists with physiological and molecular geneticists may also contribute to the understanding of genomic organization in general. Such basic research needs to be initiated now to lay the foundations for major genetic improvement of farm animals in the 21st century.

BIOCHEMICAL AND PHYSIOLOGICAL GENETICS

A.A. Grunder

The improvement of economically important traits in animals has been dominated by an empirical and statistical quantitative approach. Many advances have been recorded as already discussed. Nevertheless, breeders in more recent years have realized that there is an underlying molecular basis for genetic control of production traits. They have now become aware of the possibilities of incorporating biochemical and physiological genetic information into their selection programs. The discovery of inherited variations in blood groups in cattle by Stormont et al. (1945) and in chickens by Briles (1949) excited animal breeders because such genetically controlled variation could be used to aid in animal improvement.

This review covers the genetically controlled biochemical and physiological traits that are associated with differences in production capabilities and predicts the future role of physiological genetics in animal breeding. Lack of space, rather than lack of importance, restricts the number of blood groups and protein and enzyme polymorphisms that are discussed here.

Genetically controlled physiological traits and production

The discovery of the various blood groups in animals was followed by studies of associations between their genotypes and productivity. Briles and Allen (1961) observed that rate of egg production was affected by the *B* blood group genotypes in three of seven inbred lines; homozygosity was associated with the lower laying rate. In a study of the Dutch Black and White cattle breed, Kraay (1968) found that allelic frequencies differed between bulls and cows for the *A* and *F-V* blood group systems and suggested selection as the cause of the differences. Despite these associations between production and blood groups, the latter are not used directly in selection programs to improve production. The associations are too weak to generate significant potential for improvement beyond that achieved with conventional selection methods.

After the development of zone electrophoresis by Smithies (1955) to elucidate genetic variation in the haptoglobins of humans, many nonenzymatic protein polymorphisms have been found in farm animals and poultry since the early work of Ashton (1957) in cattle transferrins and Kristjansson (1961) in pig hemopexins. As in the work with blood groups, investigators looked for associations between protein polymorphisms and production. For example, Ashton and Hewetson (1969) studied the association between transferrins and milk production in cattle, and Rahman and Konuk (1977) studied transferrins and weight gain in sheep. The findings in a recent report by Rashid (1982) concerning the effects of ovotransferrins on economic traits in domestic fowl are typical. No correlation was found between transferrin genotypes and age at sexual maturity nor was any additive effect on egg number and egg weight observed. However, the Tf^{B} allele was associated with a body weight superior to that associated with the Tf^{A} allele. Nonenzymatic protein polymorphisms are not used to improve production traits.

Like the studies of protein polymorphisms, associations of enzymatic proteins with production have not been encouraging. In a thesis by Mina (1978) as cited by Sheldon (1980), a literature review of poultry revealed the following associations of allozyme loci and production traits: four loci with embryonic mortality, five with egg production, three with egg weight, two with viability, one with body weight, and one with fertility. However, for each of these traits except embryonic mortality, other studies reported no significant association between the three to six loci involved and the trait. These inconsistencies are exemplified by the results of Grunder and Merritt (1977) who examined a polymorphic serum esterase and traits of meat strains of chickens. After comparing traits of various genotypes with each other, they found that only five of 106 comparisons were significant, i.e., about the number expected by chance. Therefore, despite their known and defined biological function, enzyme polymorphisms are not used in selection for production.

Many poultry scientists and researchers interested in laboratory animals have selected certain lines for a specific physiological trait. These lines are used to gain better understanding of the genetic and biochemical aspects of the trait. Sheldon (1980) has listed many of these lines for poultry and has suggested that almost any trait can be changed by selection. Informative studies have also been done to identify physiological changes that occur when lines are subjected to divergent selection for production traits. One example is discussed here.

Lines of Leghorn chickens were selected for a high (THK) and low (THN) percentage of egg shell (Buss et al. 1977). Clagett et al. (1977) showed that hens of the THK line had more total serum calcium yet less total calcium in the excreta than hens of the THN line. Knowing that vitellogenin is the main factor controlling calcium binding in plasma (Deeley et al. 1975), Grunder et al. (1980) found more vitellogenin in the serum of THK-line hens than in that of THN-line hens. Also, after hens were injected intramuscularly with estradiol benzoate, those belonging to the THK line had greater increases of nondiffusible calcium in plasma, as well as greater binding of calcium by vitellogenin than those from the THN line.

All strains differing in production traits probably differ in physiological traits. To the extent that pleiotropic genes control both types of traits, knowledge of the easily measured physiological phenotypes should prove useful as an indirect means of selection for production traits.

Disease resistance and physiological genetics

The association of the *B* blood group system of chickens with viability has been recognized for some time (Gilmour 1954). The finding of a relationship between the *B* blood group and the immune system (Schierman and Nordskog 1961, Craig and McDermid 1963) may explain this association. It has been recognized as the major histocompatibility system in poultry. Hansen et al. (1967) reported that mortality among progeny with B^{21} was about half the mortality among progeny with B^{19}. Since then the involvement of *B* locus alleles with resistance to Marek's disease has been well documented (Longenecker et al. 1976, Briles et al. 1977, Okada et al. 1977) and this trait has been used successfully to select against susceptibility to this disease. This example is perhaps the only known case of a genetically well-understood trait used by the breeding industry in indirect selection against susceptibility to a disease.

The *R* blood group system in chickens was investigated in relation to resistance to lymphoid leukosis. The presence of *R* antigen on red cells was associated with the susceptibility to subgroup B virus (Crittenden et al. 1970).

As mentioned earlier, porcine stress syndrome is characterized by sudden death in pigs subjected to stress, frequently caused by physical exertion. Rasmusen and Christian (1976) showed that two genotypes of the *H* blood group system are associated with susceptibility and at least three genotypes are associated with freedom from the syndrome. It has already been mentioned, in the earlier section on swine, that the *H* blood group system and the phosphohexose isomerase system can be useful in improving meat quality (color score) (Andresen et al., 1979). Therefore, this blood group system as well as the enzyme polymorphism could be used to cull breeding stock.

The genes that control the lymphocyte antigens in mice and humans are involved in immune mechanisms and might be expected to have similar relationships in livestock. In fact, lymphocyte antigens controlled by multiple alleles at various loci have been discovered in cattle (Caldwell et al. 1977), sheep (Millot 1978), swine (Vaiman et al. 1970), and horses (Lazary et al. 1980). As with blood-group antigens, investigators searched for associations of these genetically controlled antigens with economically important traits, mainly those that are disease related. Indications of such associations have been found in cattle with eye carcinoma (Caldwell and Cumberland 1978), lymphosarcoma (Bortolozzi and Hines 1982), and mastitis (Solbu et al. 1982). Association of sheep lymphocyte antigens and scrapie is mentioned in the section on disease resistance genetics. It has already been mentioned that swine lymphocyte antigens are associated with performance levels in economically important traits. This type of investigation, especially that exploring associations with disease resistance in livestock, is very promising.

A muscle disease of meat-type chickens and turkeys called degenerative myopathy of the *Musculus supracoracoideus* (DMS) could be considered a stress-induced disease (Siller et al. 1979, Dickinson et al. 1968). Harper et al. (1975) have shown that susceptibility in turkeys is controlled by multiple genes and that DMS affects mainly adult stock. Siller et al. (1979) have shown that DMS can be induced by exercise of the wings. In studies on levels of creatine phosphokinase (CK) in the plasma of turkeys, Hollands et al. (1981) demonstrated that CK levels 4–6 days post-exercise were significantly higher in those birds in which DMS has been induced than in birds found not to have DMS. Heritability of incidence of DMS in chickens has been estimated to be 0.48 (Hollands et al. 1986). By exercising wings and measuring plasma CK, live birds susceptible to DMS can be identified and culled.

The future

The number of genetically controlled blood group systems, proteins, and enzymes is immense in poultry and livestock and one has to ask how they can be used to improve production efficiency. They will continue to be used in pedigree verification, as long as this documentation is deemed to be important in cattle (Stormont 1951), horses (Stormont and Suzuki 1965), other types of livestock, and in verification of lines of chickens (Briles 1960). The production of meat, milk, eggs, wool, and down in the most efficient manner will continue to depend on programs of various design for the simultaneous selection for multiple traits. The use of genetic polymorphisms in indirect selection will depend on cost-benefit analyses or on an assessment such as that suggested by Dickerson (1976). The improvement of meat quality through selection for the *H* blood group substance and phosphohexose isomerase in swine has been discussed earlier. Unlike humans, particular polymorphisms that convey low fitness to animals, such as riboflavin deficiency in chickens (Maw 1954), are quickly lost, and therefore such information is more applicable to human medicine than to animal breeding.

An important application of physiological genetics will be in breeding for resistance to disease. Clearly, breeders are reluctant to expose valuable breeding stock to disease agents. Therefore, use of the *B* blood group system to select against Marek's disease in chickens will continue. Efforts should be made to find other indirect markers or physiological genetic traits useful in selection against susceptibility to infectious diseases. Frequency of stress diseases in swine and poultry probably can be reduced by applying information about correlated physiological parameters. Such information should be particularly applicable to animals selected for artificial insemination studs or intensely selected sire lines.

There are suggestions that polymorphisms should be sought in tissues other than the very accessible blood tissue. Robertson (1966) suggested looking in tissues with high synthetic activity such as the liver or mammary gland. Lewontin (1978) suggested that breeders should study the regulator genes rather than the structural genes so as to use biochemical variation to predict the outcome of artificial (and natural) selection. Variation in blood groups, proteins, and enzymes that is explained by major gene loci is assumed to be determined by structural genes. The physiological variation for hormone and enzyme levels is probably based on regulator genes. Because most production traits are quantitative, variation in the products of regulator genes can be used in predicting production performance. Such variation will have to be sought in tissues other than blood.

In the search for traits or markers either directly or indirectly useful in the genetic improvement of farm animals and poultry, biochemical and physiological genetics could be expected to contribute to the elucidation of many genetic and epigenetic processes. New knowledge of this kind will be useful in bridging the large gaps that now exist among the phenomena and concepts dealt with by the molecular and quantitative geneticists.

DISEASE RESISTANCE GENETICS

J.S. Gavora

Diseases can be broadly categorized as genetic, such as developmental, metabolic, and physiological disorders; infectious; and stress related. The first category is, at least partly, dealt with earlier. Some genetic disorders are the pale, soft, exudative meat and the sudden death syndrome in swine and the degenerative myopathy in turkeys and chickens already mentioned. Extreme selection for high growth rate and body conformation, as practiced mainly in broiler chickens, turkeys, and swine, seems to lead to developmental and physiological problems of which these disorders are examples. In addition, morphological problems, exemplified by syndromes generally referred to as leg problems, and a reduced reproductive capacity are observed with increasing frequency in meat-type animals. The remedy for these problems will probably be the restoration of physiological balance in these animals through multiple-trait selection for physiologically and economically important characters. Unfortunately, strong competitive pressures often force breeders to continue to select for one or two economically important traits and thus to perpetuate and aggravate the problems. Although a number of other genetic disorders of this kind exist in domestic animals and poultry (Mulvihill 1972), they are usually simply inherited and can be relatively easily eliminated through selection.

With the exception of the disorders mentioned in meat-type animals, there have been no serious genetic problems in the past two decades. Therefore, this review is limited to a discussion of genetic resistance to infectious diseases broadly defined as the ability to resist any alterations of the state of the body by external causes that interrupt or disturb proper performance (Gavora and Spencer 1978), and of resistance to stress, where stress is defined as external body forces that tend to displace homeostasis (Scott 1981).

As mentioned earlier, traits for cost reduction are historically the most recent characteristics to have received attention by animal breeders, and disease resistance was among the latest traits within the group to be dealt with seriously. Notable exceptions, such as the development of breeds that are tolerant to *Trypanosoma* ssp., in cattle, sheep, and goats (FAO 1980, Murray and Trail 1982) confirm rather than negate this observation. The degree to which artificial selection has contributed to the trypanotolerance of breeds such as N'Dama cattle is uncertain.

There are several reasons why animal breeders have paid relatively little attention in the past to breeding for disease resistance. Hutt (1958), considered by many to be the father of disease-resistance genetics, pointed out that plant breeders had taken advantage of genetic resistance to a much greater degree than have animal breeders. The difficulty in assembling the necessary multidisciplinary expertise given the long-standing reluctance of animal geneticists and veterinarians to work together is one possible reason. An additional obstacle is the high cost of breeding for disease resistance. Losses from exposure of test groups to pathogens being used to measure resistance can be heavy. In the past decade, the situation has gradually improved. Increasing amounts of research and the beginnings of practical application of its results are now being seen in animal and poultry breeding. This trend will likely continue. The reduction of losses achieved through improved disease resistance will allow increasing production without a need for new land resources (Gavora 1982), which is a consideration of growing importance for our overpopulated planet.

Improvements in disease resistance

Despite the bleak picture painted here, there has been some progress. Efforts to improve disease resistance globally are steadily increasing. The following examples should illustrate and document this claim.

Cattle A successful attempt to reduce the damage in cattle from tick infestations, which are estimated to cost $40 million annually in Australia, was reported by Utech and Wharton (1982). Heritability of resistance to ticks ranges from 40 to 80% (Hewetson and Nolan 1968, Wharton et al. 1970, Seifert 1971). The reduction in the number of ticks as estimated by tick mortality on one side of the body of test bulls increased from 89 to 99% by selection of the bulls (Utech and Wharton 1982).

The situation in mastitis, losses from which are estimated at $2 billion annually in the United States alone, was recently reviewed by Miller (1982). He concluded that the lack of a suitable criterion for the detection of mastitis in the field is a major obstacle for its control. A heritability of 0.1–0.2 for mastitis resistance indicates that this disease may be subject to genetic control. Increasing knowledge of the resistance mechanisms involved and the development of new diagnostic methods give hope for future improvements in the control of mastitis.

Sheep The etiology and nature of the pathogen causing scrapie in sheep are not completely understood. The pathogen is generally referred to as a slow virus but has been also described as a geneless virus (Lecocq 1982), viroid, and even a voodoo (Marsh et al. 1978). Scrapie is a degenerative disease of the nervous system, which occurs as natural infection in sheep and goats (Dickinson 1976). It resembles the human diseases Kuru and Creutzfeld-Jacob disease.

A protein is apparently required for infection and a new term, *prion*, was introduced to identify the unusual infectious particles (Bolton et al. 1982). According to Kimberlin (1979), the agent seems to be transmitted by both maternal and horizontal routes. Specific susceptibility to experimental infection with at least one source of disease agent is controlled by a single gene, for which susceptibility is dominant. Variation in the course of the disease reflects genetic differences among hosts and strains of the agent. Different scrapie syndromes can be produced within a single host genotype by different scrapie agent strains (Dickinson 1976).

Unlike about 200 years ago when it was a serious problem in Britain (Dickinson 1976), scrapie is not now a highly costly disease. The genes known or suspected to be involved in scrapie resistance in sheep confer resistance to some strains of the disease agent but not to others. Dickinson and Fraser (1979) therefore recommended that genetic methods should be used to ameliorate high-incidence situations rather than as a means of eradication. The possibility of association of scrapie resistance with some haplotypes of the major histocompatibility complex of sheep (OLA), reported by Millot et al. (1982), may be another avenue for future research.

Swine After Sellwood et al. (1975) reported that K88-positive *Escherichia coli* do not adhere to the intestine of all pigs, Gibbons et al. (1977) found that the presence of the receptor is determined by a single locus with two alleles. The test for presence of the receptor, involving typing intestinal cells obtained by biopsy, makes selection for this type of *E. coli* resistance practical. This test is being used in swine breeding (Walters and Sellwood 1982) to control the economically greatly damaging diarrhea associated with *E. coli* in piglets.

Chickens The chicken often serves as the laboratory species among farm animals because of its low price, high rate of reproduction, and short generation interval. Compared with most laboratory animals, it has the added advantage of being an economically important species.

Probably the best example of successful research on disease resistance is the work on Marek's disease, a lymphoproliferative, highly lethal, and costly disease caused by a herpes virus. Genetic resistance was the only means of control for the disease up to 1970. The development of vaccines against Marek's disease, which represent the first effective vaccines against a neoplastic disease in any species (Churchill et al. 1969, Kawamura et al. 1969, Witter et al. 1970, Biggs et al. 1970), substantially reduced the devastating losses from the disease. Gavora and Spencer (1979), however, demonstrated that both vaccination and genetic resistance are required for maximum protection against the disease.

Starting from the classical work at Cornell University (Hutt and Cole 1947), resistance to Marek's disease has been shown repeatedly to be rapidly improved by selection. This improvement can be achieved simultaneously with improvement of multiple production traits (Gavora and Spencer 1983). Direct selection was used successfully by commercial poultry breeders to improve Marek's disease resistance mainly before the development of vaccines. As mentioned previously, since the discovery that resistance is associated with the B^{21} haplotype of the major histocompatibility complex of the chicken (Hansen et al. 1967, Longenecker et al. 1976, Briles et al. 1977), poultry breeders have also used indirect selection for improving resistance to Marek's disease. The resistant haplotype, or at least a part of it (Hala et al. 1981), is detectable on red blood cells, and commercial poultry breeders are now increasing its frequency in their stocks (Gavora et al. 1986).

Another viral lymphoproliferative disease of chickens that received increased attention in the past decade is lymphoid leukosis. It is transmitted both congenitally and horizontally, and the mechanisms of resistance to this disease are well understood (Crittenden 1975). The disease normally causes only very low mortality. It was not considered important until subclinical infection with the virus was proved to induce severe negative effects on practically all production traits, to greatly increase the mortality from causes other than the disease itself, and to have serious consequences in selection for high performance (Spencer et al. 1979; Gavora et al. 1980, 1982*b*, 1983; Harris et al. 1983; Gavora and Spencer 1985). These findings along with the development of effective methods for virus detection (Spencer et al. 1987) prompted most of the world's commercial poultry breeding companies to initiate eradication of the virus.

Prospects for genetic improvement of disease resistance

Dramatic increases in immunological research are resulting in a rapidly growing understanding of immune response. In particular, the results from the Biozzi group (Biozzi et al. 1979) allow assessment of the prospects for a generalized improvement of disease resistance. A generalized approach is important because to select for specific resistance to each pathogen is not realistic. The increased understanding of the role of the major histocompatibility complex in the immune response of all animal species (Simonsen 1982) will likely play an important role in the future effort to improve the survival of farm animals. In the search for general resistance mechanisms, researchers should not neglect such nonimmunological mechanisms as lysozyme (Tizard 1982) and interferon (Stewart 1979) which have a broad spectrum of potentially protective effects.

Gavora and Spencer (1978, 1983) have argued repeatedly that genetic resistance to disease has a significant role to play in addition to, and in combination with, all other means of disease control. In populations from which a pathogen has been eradicated, genetic resistance provides a safeguard in case the pathogen should reappear; genetic resistance in combination with vaccination provides optimum protection; and genetic resistance is an animal's only protection against drug-resistant pathogens. In addition, pressures exerted by consumer groups are expected to force a reduction in levels of medication administered to food-producing animals. Such restrictions will further emphasize the importance of genetic resistance and disease eradication in farm animals and poultry.

Indirect selection for general resistance to disease, based on immune response and other marker traits that do not require exposure to pathogens for their expression, appears to be the preferred long-term strategy for breeding disease-resistant animals. Nevertheless, because of our insufficient understanding of the complex mechanisms and relationships involved, both direct and indirect selection and heterosis will likely be used in the future.

Research will continue to be needed to complement results from medically oriented studies and to adapt them to animal breeding, as well as to investigate areas of interest unique to animal breeders. In addition, resistance mechanisms must be better understood and the relationship of resistance to various diseases with production traits must be elucidated to allow proper incorporation of improvements in viability in animal breeding plans. Molecular genetics is opening completely new avenues for animal improvement, and genetic mechanisms of resistance are among the prime candidates for its application.

GENETIC IMPROVEMENT USING NEW REPRODUCTIVE TECHNOLOGIES

J. Nagai

Reproduction is important for the maintenance of superior stocks over successive generations. Increasingly superior stocks can be produced by selection and mating. The rate of reproduction as well as the generation interval are major factors in determining the rate of genetic improvement. Moreover, performance in some species can only be measured when animals reproduce. For example, lactation normally begins when a cow calves: until this time, milk-producing capacity cannot be assessed. The number of genes involved with reproduction and the expression of these genes are not well known. However, the rate of genetic gain can be increased by increasing the reproductive rate. The effects of advances in reproductive technologies on genetic improvement of livestock are reviewed, placing emphasis on methods for increasing the low reproductive rates of livestock such as cattle and sheep.

Artificial insemination

The techniques for collection, dilution, storing, and insemination of semen have been applied effectively to livestock, particularly to dairy cattle (Foote 1981). The major advantage in using AI is the genetic improvement in performance through intensive use of semen from proven sires. Indeed, AI and progeny testing have contributed greatly to the genetic improvement of dairy cattle. Studies on dairy cattle in this area include those on bovine acrosin, which is thought to assist the sperm in penetrating the zona pellucida around the ovum (Lunstra and Echternkamp 1982, Elce and McIntyre 1982); movement of bull spermatozoa in cervical mucus (Katz et al. 1981); daily spermatozoal production *in vivo* (Weisgold and Almquist 1979, Almquist 1982); cryopreservation of spermatozoa (Jeyendran et al. 1981, Foote 1982); separation of live and dead sperm (Landra et al. 1980); cytometry for assessment of X- and Y-sperm populations in cryopreserved semen (Garner et al. 1983); and genetic effect on libido and mating ability (Chenoweth 1983). In beef cattle and sheep, AI is not widely used in either Canada or the United States. However, research on AI with these animals is in progress. For example, studies have been done on the effect of time of AI on the fertility of ewes (Langford 1982). As research advances, the results are expected to become more dependable and new techniques will be developed for the successful application of AI in beef cattle and sheep.

Estrus detection, synchronization, and superovulation

The major factors causing low efficiency of reproduction in dairy cattle are low rates of conception and delayed first service (Pelissier 1976). To resolve these problems techniques necessary for the detection of estrus have been studied and improvements proposed (Barr 1975, Appleyard and Cook 1976, Stevenson and Britt 1977, Williams et al. 1981). Similarly, to alleviate problems caused by difficulties in the detection of estrus, techniques for synchronization of estrus have been studied intensively. Synchronization and superovulation have been made possible by treatments with hormones such as prostaglandin, PGF2α, and a luteolytic hormone (Gordon 1982). These techniques are used effectively in embryo transfers. Studies have also been made on ovarian activities to determine the effects on superovulation of various treatments with hormones such as gonadotropin-releasing hormone (Carter et al. 1980, Garverick et al. 1980, Ainsworth et al. 1982). Advances in this area are leading to a more effective use of oocytes from genetically outstanding females, particularly from cows and ewes.

Embryo transfer and cryopreservation of embryos

A new technology, whereby fertilized eggs and embryos collected from donors are transferred into the uteri of recipients (Seidel and Seidel 1982, Adams 1982, Hafez and Semm 1982), has been applied to cattle (Newcomb 1982), sheep (Moore 1982), and goats (Armstrong et al. 1983). Embryo transfer (ET) can improve the rate of genetic gain, particularly in livestock with low prolificacy such as dairy cattle (McDaniel and Cassell 1981). Data on the progeny of donor cows should be considered in the evaluation of those cows but the time required to obtain such information is rather long (Powell 1981). Van Vleck (1981) stated that the small increase in accuracy in evaluating a dairy cow by testing her progeny would not justify the increase of 3 or 4 years in generation interval that would ensue. He suggested that increased selection intensity for dams of sons is a possibility but noted that the difficulty with the evaluation of dams of sons must still be overcome. The advantages of using ET appear to be small, at least in schemes in which intense and accurate selection is already practiced among cows that are used to produce bulls (Hill and Land 1976). However, the advantages could be realized in a small herd (Robertson 1954, Land 1977*a*, Church and Shea 1977). Recently, Nicholas and Smith (1983) proposed methods that combine the use of ET with sib tests and pedigree information, which reduce generation interval and which tolerate less accuracy of selection. This concept of a nucleus herd (Nicholas and Smith 1983) shows promise for a significant increase in rate of genetic gain but needs experimental verification. A big problem with ET at present is cost that ranges from $300 to $2000 per transfer. This cost must be reduced drastically before the technique can be used widely (Wilmut and Hume 1978, van Vleck 1981). Techniques for freezing ova and embryos are now suitable for field use (Maurer 1978, Leibo 1981) but some problems, such as low pregnancy rate in cattle when frozen embryos are used (Kanagawa 1983), have been noted.

Off-season breeding in sheep

Under natural conditions, sheep mate in the fall. With proper management of reproduction, however, year-round mating has been made possible (Heaney et al. 1980). Progestagen and pregnant mare's serum gonadotropin have proven useful for routine synchronization of estrus (Hackett et al. 1982). New techniques have been evaluated for selecting ewes with superior reproductive rate (Bindon and Piper 1979). Among important reproductive traits in sheep are litter weight and number of lambs born (litter size). The litter weight is positively associated with the number of lambs born, and both traits are heritable. Litter size can be increased by selection and crossbreeding. The lifetime production of a ewe may be measured by the total body weight of all the litters she produces. This measurement is affected by the number of parturitions and by the size and weight of all the litters she produces. Combined efforts to improve reproduction, genetic makeup of the animals, and their management would yield a substantial increase in the lifetime production of a ewe.

Lifetime (herd-life) performance in dairy cattle

Normally, favorable heterosis occurs in reproductive traits when two breeds or strains are crossed. This hybrid vigor can result in superior long-term performance involving reproduction. Crossbred cows are superior in lifetime (herd-life) milk production because of heterosis in days from first breeding to conception, calving interval (McDowell et al. 1974), and embryonic mortality (Ayalon 1978). The effect of heterosis on lifetime performance is being examined under the national cooperative dairy cattle breeding project carried out at the Animal Research Centre in Ottawa and at collaborating research stations of Agriculture Canada (McAllister et al. 1978). It appears that heterosis exists for survival, growth, heifer reproduction, and lactation yields. Genetic aspects of lifetime performance have been investigated in dairy cattle (Hoque and Hodges 1980), with particular emphasis on fertility (Hansen 1979, Berger et al. 1981, Philipsson 1981), and also in mice. Nagai et al. (1980) found that lifetime lactation in F_1 crosses of mouse lines derived from different populations was superior to that in F_1 crosses of lines derived from the same population by 18%. Similarly, number of lactations, a component trait of lifetime lactation, was found to be superior by 14% and another component trait, milk production per lactation, was superior by 4%. Crossbreeding systems that are practically applicable in dairy cattle include crisscross (CC) matings and repeat hybrid male cross (RHMC) matings (Nagai and McAllister 1982), as well as random mating within a population synthesized from various breeds (SYN). Mouse experiments revealed that the expected lifetime performance ratio of CC/RHMC or CC/SYN was in excellent agreement with the observed ratio (Nagai and McAllister 1983).

Genetic gain from new reproductive technologies

The rate of genetic improvement in animals is determined by the accuracy with which the breeding values of sires and dams are estimated, the selection intensity, the genetic variation among individuals, and the length of generation interval. Advances in reproductive technologies will contribute to genetic improvement by implementing some of these factors. The ability to determine the sex of semen and embryos (Bongso et al. 1978, Betteridge et al. 1981, Ohno 1983) will help to increase selection intensity. Application of procedures for splitting embryos will allow production of monozygotic twins (Ozil et al. 1982) and monozygotic quadruplets (Willadsen 1982). When the breeding values of animals supplying the embryos are estimated accurately, the splitting of embryos from superior parents can expedite genetic improvement. Genetically superior individuals could also be multiplied by cloning or parthenogenesis (Markert and Seidel 1981) or by combination of two X-bearing gametes of a male, i.e., selfing (van Vleck 1981). By removing the pronucleus of fertilized eggs, genetically homozygous females can be produced in one generation (Hoppe and Illmensee 1977, Clement and Petters 1977). Techniques of superovulation (Elsden et al. 1978, Chupin and Procureur 1983), *in vitro* fertilization (Brackett 1981, Ball et al. 1983), and embryo transfer (Adams 1982) will allow the use of innumerable, otherwise unused, follicles in the ovary for producing young.

Techniques for freezing, thawing, and transferring embryos could be used in the establishment of embryo and gene banks. Techniques for transplanting a nucleus (Illmensee and Hoppe 1981) and inserting a specific gene into embryos (Constantini and Lacy 1981, Wagner et al. 1981, Palmiter et al. 1982*a*) could be developed further to improve animal performance in traits controlled by multiple genes. Interspecies and intergenus chimeras (for example, an individual containing cells from both a sheep and a goat) could be used to generate new types of animals adaptable to harsh environments. Priming pheromones (Izard and Vandenbergh 1982) or chemically defined male odor (Sasada et al. 1983) could be used for effective reproductive management. Attempts have been made to control day of parturition by treating animals with PGF2α (Butler and Boyd 1983). New management programs could be initiated, such as a system whereby estrus of animals is detected by body heat (Hurnik 1983) and the animals are inseminated by sexed semen released from a capsule previously embedded in the reproductive tract.

Although problems of animal ethics and animal welfare will be matters of discussion, the advances achieved in the past decade suggest that enormous further advances in future reproductive technologies can be expected. The rate of genetic improvement in animals will be much faster in the future when breeding plans capitalizing on advanced reproductive technologies are promoted.

MOLECULAR GENETICS

D.E. Bernon and J.S. Gavora

Several reviews have dealt with the potential values of both molecular and reproductive biology in future animal improvement (Church 1974, Ward 1982, Rutledge and Seidel 1983, Wagner 1985, Crittenden and Salter 1985, Teather 1985, and Church et al. 1985). Related aspects of reproductive biology were the subject of the previous discussion here. Nevertheless, molecular genetics should be viewed only as one component of modern genetic engineering. This field is broadly defined by Rutledge and Seidel (1983) as those technologies either that permit direct changes in the frequency of gene or genotype or that change the characteristics of the life history of individuals or their gametes such that some individuals can make a disproportionate contribution to the gametic or zygotic pool of the population. In general, any application of knowledge to genetic change is genetic engineering. Thus, even conventional, quantitative genetics applied to animal improvement qualifies as genetic engineering (Dickerson and Willham 1983). The modern technology discussed here represents only one set of the more advanced and potentially effective tools that can be applied in the engineering effort.

To date, animal breeders have used mostly only naturally occurring genetic variation as the basis for improvement. With the potential offered by molecular genetics and related approaches, the breeder may be able to control and create new genetic variation. Also, advances in molecular genetics are rapidly expanding our knowledge of genetic organization. Recent disclosures are challenging our historical views on evolution and genetic diversity (Gillings and Frankham 1982), and the rate of acquisition of new knowledge in this area shows no sign of slowing down (Ward 1982).

The gene structure of vertebrates, which is the object of animal breeders' efforts, seems to differ from that of prokaryotes, as originally elucidated by Jacob and Monod (1961). One distinguishing element is the presence of DNA sequences (introns) that interrupt the coding sequence rather than coding for polypeptides. The presence of introns within structural genes ranges from none to situations where most of the gene-coding sequence consists of introns. For example, only less than 5% of the human myoglobin DNA structure codes for message (Lewin 1983). A similar situation exists in milk protein genes. For example the gamma casein gene of the rat is 17 times longer than its mRNA and has nine small coding sequences (exons), one of which is only 44 bases long (Kang et al. 1986). Also, the arrangement of genes in some instances seems to reflect the order of their expression (Ward 1982). These and other similar characteristics of the eukaryote genome have to be borne in mind when direct manipulation of the genome is attempted.

Techniques

The following steps for modification of the genetic makeup of an animal were identified by Robertson (1982). The gene concerned is first isolated, so that it can be multiplied in a bacterial cell or in some equivalent host. The sequence is best isolated in the form of mRNA in tissue where the gene is switched on. Then, after processing, the gene is inserted into recipient animals in such a way that it is expressed in the right tissue and is transmitted stably to subsequent generations.

For identification of the gene of interest, its exact position on the relevant chromosome need not be known; because the functioning DNA can simply be removed from the tissue of interest, sequenced, multiplied, and transferred (Wagner et al. 1981; Palmiter et al. 1982*a*,*b*; Rubin and Spradling 1982). In the identification process, an understanding of chromosome banding patterns, of linkage groups, and of the exact structure of the gene product could be helpful.

Examples of genes successfully identified include the ovoglobulin and ovalbumin genes in poultry (Bloom 1981, Somes 1981), the keratin genes in sheep (Ward 1982, Ward et al. 1982), and rosy gene in *Drosophila* (Rubin and Spradling 1982, Spradling and Rubin 1982).

Most work on multiplication of the recovered DNA is done with *E. coli* (Strasiak and Capua 1982). The cloning of genes for known gene products before they are transferred increases the amount of material available (Padyatty et al. 1981) and allows its characterization (Choo et al. 1982, Edgell et al. 1979).

Three different methods have been proven effective in gene transfer (Ward 1982): first, the transfer with the aid of vectors derived from transforming viruses; second, the transformation of cell culture lines with naked DNA; and third, the direct microinjection of purified DNA.

The successful use of virus lambda vector to insert genetic material into *E. coli* was reported by Williams and Blattner (1980) and Lindenmaier et al. (1982), although this vector can apparently only transduce genes near its attachment site (Shimada et al. 1977). Similarly, recombinants of the SV40 virus were used by Hemer (1980) to introduce foreign genes into animal cells. Recently, Salter et al. (1986) reported a successful gene transfer in chickens, using engineered avian retroviruses.

Microinjection appears promising for animal applications. Celis et al. (1980) pioneered this method in which a tip of a micropipette (1 µm in diameter) is inserted through the membrane of a living cell. This technique has been used to transfer the rabbit globin gene into mice (Wagner et al. 1981), Constantini and Lacy 1982), the agouti gene from mouse to mouse (Stewart and Mintz 1981), the rat growth hormone gene into mice (Palmiter et al. 1982*a*,*b*), and the human globin gene into mice (Stewart et al. 1982). Recent examples of gene transfers by microinjection were provided by Hammer et al. (1985) for rabbits, sheep, and swine, by Brem et al. (1986) for swine, and by Ward et al. (1986) for sheep.

A gene transfer is completely successful only if the new gene functions properly in the recipient and is successfully transferred to progeny. Several generations of progeny expressing the new gene further document the stability of the transferred genetic material.

At least for some time to come, genetically modified individuals will have to be conventionally reproduced. Their integration into breeding populations opens up further possibilities for the combination of conventional methods of breeding with these new methods and will provide new areas for research and its applications. Clearly, before transgenic animals and birds are used in industrial livestock production, they have to be thoroughly tested. It is essential to gain understanding of the behavior of the exogenous genes and their effect on overall performance. This testing will require substantial resources both in expertise and experimental facilities – an added cost of biotechnology applications that is often forgotten by planners.

Eventually, more direct methods for the propagation of highly desirable genomes, such as embryo splitting, cloning, and sexing, may become practically feasible (Church et al. 1985). When these new methods are achieved, animal production techniques will bear little resemblance to those in use today (Ward 1982).

Potential applications

The techniques of modern genetic engineering can be applied to animal improvement in several ways.

Transfer of genes Genes that are potentially more desirable than those existing within the individual can be transferred from within or outside the species. An example of such a gene transfer was provided by Palmiter et al. (1982*a*) who transferred rat growth hormone genes to mice and thus induced a dramatic increase in their body size. The rat growth hormone gene was fused to a metallothionein gene before it was transferred into mice, to provide a mechanism for controlling of the expression of the new gene. Earlier, a rabbit globin gene was sucessfully transferred into mice (Wagner et al. 1981). Similar transfers for domestic animals and birds have been reported, as already mentioned. Candidates for gene transfer are the Booroola gene, associated with multiple ovulations in sheep, double-muscling genes, and others.

Besides allowing the transfers of genes across biological barriers that normally prevent crossbreeding of certain taxa, direct gene transfer by molecular techniques has at least two important advantages. First, direct transfer is much more rapid than crossing and backcrossing methods normally used to transfer a gene or a group of genes. Second, direct transfer eliminates the transfer of other, undesirable genetic material that is unavoidable with the conventional techniques. Even after prolonged backcrossing, the elimination of undesirable genetic material may remain uncertain, under conventional circumstances.

After the transfer of a single new gene into the genome, its successful expression and integration into the recipient's ontogeny and physiological processes, are definite concerns. Recent studies proving that the expression of transferred new genes is being controlled by the recipient's genome are encouraging. For example, Brinster et al. (1981) found that a transferred foreign gene was expressed differentially in various tissues in a way similar to that of genes that are a normal part of the genome.

While acknowledging the dangers of moving into the realm of science fiction, one can imagine the benefits that could accrue by using genetic engineering techniques to provide nonruminants with the ability to make use of roughage, for example. The immunoresponses controlling genes, as well as genes controlling disease resistance, may offer similar possibilities for genetic engineering in the next decade. For example, genetic engineering may allow the transfer of disease resistance or disease tolerance from low-producing indigenous breeds to modern breeds that normally suffer from locally occurring pathogens, without introducing undesirable genes associated with low productivity.

Gene transfer also opens up the possibilities of modifying the animal genome in such a way that the animals can produce large quantities of important proteins (Marx 1982).

Removal or blocking of undesirable genes Eliminating the effect of undesirable genes is another way in which molecular techniques could potentially be applied. Examples of undesirable genes are those that code for receptors of pathogens such as the viruses of lymphoid leukosis in chickens (Crittenden 1975, Payne 1985) or the K88 strain of *E. coli* in pigs (Walters and Sellwood 1982).

Endogenous lymphoid leukosis virus in chickens, for example, is produced by the birds from proviral DNA that is a permanent part of the birds' genome. Removal of such DNA or rendering it incapable of producing the virus seems a realistic goal. A mechanism referred to as antisense DNA that is a normal defense mechanism in some lower taxa, may be used to block undesirable genes (Crittenden and Gavora 1986).

Alteration of structural genes to change product quality Ward (1982) in his excellent consideration of the possible contributions of molecular genetics to animal improvement, discusses the possible changes in textile fabrics (e.g., wool, cashmere, and mohair), muscle proteins (e.g., actin and myosin), and milk proteins (e.g., caseins and lactoglobulins) and gives a detailed account of related advances in the Australian work on keratin. The possibilities to change product composition and to improve its quality or the efficiency of its production are many, and this field is wide open.

Evaluation of candidates for selection Molecular genetics may also become a tool for the identification of those animals bearing undesirable or desirable genetic characteristics. Such information could be used in conventional selection or in direct genetic manipulation.

In this respect, restriction fragment length polymorphisms (RFLP) detected by using cleavage of DNA by restriction enzymes and suitably labeled DNA probes could be used as genetic markers for important quantitative trait loci. The principles of application of RFLP in livestock improvement were discussed by Beckmann and Soller (1983), Soller and Beckmann (1983), and Smith and Simpson (1986).

Understanding the genome As mentioned earlier, despite the great advances in molecular genetics, the understanding of the genome in all its complexities is still rather rudimentary. Nevertheless, animal breeders have to deal with complex production traits and molecular genetic structures, the syntax of which is beyond our present comprehension. The problem is further compounded as the phenotypic expression of such characters involves epigenetic processes of comparable complexity. The need to deal with these complex traits and molecular genetic structures will, in the future, involve multiple techniques and scientific disciplines. The gradual elucidation of relationships that should ensue from such multidisciplinary research will benefit not only the animal producers and consumers of animal products but also the biological sciences in general. This type of research may eventually allow the manipulation of desirable gene complexes rather than of single genes. Also, the manipulation of regulatory rather than structural DNA sequences will then become possible, with important potential application in improvement of animals.

Identification of individuals or genetic groups and verification of parentage DNA polymorphisms will likely provide a new, reliable method for the identification of individuals, breeds, lines, or strains, and for verification of parentage. The method, referred to as DNA fingerprinting in humans (Jeffreys et al. 1985), may eventually replace blood typing and biochemical polymorphisms now used in verifying parentage in cattle and horses.

It was proposed recently that synthetic DNA sequences be inserted in transgenic individuals as specific tags that will enable unequivocal identification of varieties by sample assays (Beckmann and Bar-Joseph 1986). There is no reason why a similar tagging procedure could not be applied in animal breeding.

CONCLUDING REMARKS

J.S. Gavora

This review of the past and future roles of the various research areas and disciplines illustrates their continuous interplay and how their complementary development is becoming increasingly common and desirable. Recently, scientists have been emerging from the "cocoons" of their disciplines and abandoning individual research in favor of joining multidisciplinary teams. Multidisciplinary teams of experts are also getting involved in the technical management of breeding programs. As was pointed out by Rutledge and Seidel (1983), disciplines act synergistically, which makes any attempts to isolate the effects of a single new technology fruitless. However, the future contribution of the various research areas and scientific disciplines to progress in animal breeding will probably vary relative to their maturity. The expected effects of molecular genetics, biochemical and physiological genetics, and quantitative and statistical genetics are represented schematically in Figure 2.

This review of animal breeding leads to one general conclusion: the most important challenge for animal breeding research is now to find and maintain a balance between conventional breeding and genetics efforts, on the one hand, and biotechnology approaches, on

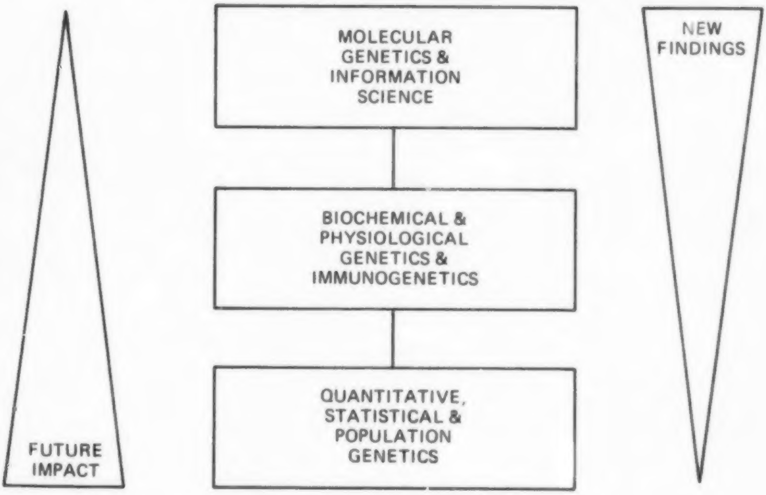
MOLECULAR GENETICS & INFORMATION SCIENCE
BIOCHEMICAL & PHYSIOLOGICAL GENETICS & IMMUNOGENETICS
QUANTITATIVE, STATISTICAL & POPULATION GENETICS
FUTURE IMPACT
NEW FINDINGS

Figure 2 **Genetic disciplines relevant for animal breeding, their expected effect on practical breeding programs, and their expected contribution to new findings.**

the other hand. Biotechnology provides animal breeders with powerful tools. The acquisition of such tools from basic research and their further development requires substantial funding. Neglect of this area would harm future improvement of livestock. However, the hasty, dramatic reduction in resources devoted to conventional research, to finance biotechnology, may be equally dangerous.

We strongly support continuation of extensive, conventional animal breeding research, including selection experiments in all livestock species. Despite recent progress in molecular and cellular manipulation, conventional breeding will remain the basic method of animal improvement. Biotechnology research has the best probability to succeed when conducted together with a strong research effort in conventional animal production disciplines by teams of experts in molecular genetics and biotechnology, as well as in traditional scientific disciplines. The challenge is to optimize the integration of biotechnology in animal breeding.

Our work on this review has caused us to appreciate more clearly the complexities faced by animal breeders. We now believe that an attempt to achieve completeness would be unrealistic. Nevertheless, we hope that, by combining a retrospective examination of the subject with a futuristic analysis, we have provided some useful information to the reader.

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